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EFFECTS OF PHOTOCHEMICAL OXIDANTS ON PLANTS

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Photochemical oxidants are found in "photochemical smog" which is a complex mixture of primary and secondary air pollutants. The photochemical oxidants are secondary air pollutants formed by the action of sunlight on nitrogen oxides and reactive hydrocarbons, their precursors. The most important phytotoxic components producted by these atmospheric photochemical reactions are ozone and peroxyacetyl nitrate. Otherperoxy compounds, aldehydes, ketones, organic and inorganic acids, aerosols, and nitrogen dioxide also are formed. An analysis and evaluation of the available literature was used to characterize the relationships among emissions, ambient concentrations, effects and to identify the important controlling influences on the formation and effects of photochemical oxidants.

The ultimate protection of humans, animals, plants, and materials from photochemical oxidant injury requires reduction of the ambient concentration of the particular air pollutant. The available emission estimates for the precursor compounds indicate that, at least for the foreseeable future, humans and the environment will continue to be impacted by photochemical oxidants. The material for this book was selected to provide a basis for preventive measures at the emission source and at the site of impact; also to provide researchers and students with a comprehensive information base

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PREFACE

Photochemical oxidants are found in "photochemical smog" which is a complex mixture of primary and secondary air pollutants. The photochemical oxidants are secondary air pollutants formed by the action of sunlight on nitrogen oxides and reactive hydrocarbons, their precursors. The most important phytotoxic components produced by these atmospheric photochemical reactions are ozone (O_3) and peroxyacetyl nitrate (PAN). Other peroxy compounds, aldehydes, ketones, organic and inorganic acids, aerosols, and nitrogen dioxide also are formed. An analysis and evaluation of the available literature was used to characterize the relationships among emissions, ambient concentrations, effects and to identify the important controlling influences on the formation and effects of photochemical oxidants.

The biological activity of photochemical oxidants was first clearly manifest during the early 1940s when vegetation injury was observed in the Los Angeles Basin in the United States. Since that time, as a consequence of the increasing emissions of the photochemical oxidant precursors, nitrogen oxides and reactive hydrocarbons, the photochemical oxidants have become the most important air pollutants in North America. In other parts of the world, for example South and Central America, Asia, and Australia, photochemical oxidants threaten vegetation, particularly the economic and ecological performance of the plant life. Based on current knowledge, photochemical oxidants should be considered as a primary cause of the new type of forest injury presently found in Central Europe.

The first chapter of this book, "Formation, Transport, and Control," will identify emission sources of the photochemical oxidant precursors, the physical-chemical reactions in the ambient air that form the photochemical oxidants, and the influence of major environmental factors controlling their formation. Suggestions for reducing the ambient exposures from photochemical oxidants are given.

The section, "Effects of Photochemical Oxidants on Plants," discusses the impacts of the most important phytotoxic components, ozone and PAN, at the cellular, organal, organismal, plant community, and ecosystem levels, in relation to pollutant uptake, differential plant resistance, as well as the influence of the internal and external growth factors that modify the responses. Methods for detecting and evaluating air pollutant effects are reviewed. The dose-response relations were used to derive air quality criteria which can provide an important perspective for developing air quality standards.

The original scope of this publication included a section on "Effects of Photochemical Oxidants on Humans and Animals." However, a book published in 1983 reviewed this topic in detail, "The Biomedical Effects of Ozone and Related Photochemical Oxidants," Volume V, SD Lee, MG Mustafa, MA Mehlman (eds), Princeton Scientific Publishers, Princeton, New Jersey, USA, pp. 643.

The ultimate protection of humans, animals, plants, and materials from photochemical oxidant injury requires reduction of the ambient concentration of the particular air pollutant. The available emission estimates for the precursor compounds indicate that, at least for the foreseeable future, humans and the environment will continue to be impacted by photochemical oxidants. The material for this book was selected to provide a basis for preventive measures at the emission source and at the site of impact. Another objective was to provide the increasing numbers of researchers, teachers, and students with information about photochemical oxidants and their effects.

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CHAPTER 1
INTRODUCTION

Although numerous secondary components occur in the photochemical smog complex (Part 1), only the most important phytotoxic components, ozone (O_3) and peroxyacetyl nitrate (PAN) are discussed. Phytotoxic concentrations of ozone are more widely distributed and generally occur in higher ambient concentrations than do those for PAN. However, on volume (molecular) basis, PAN is more phytotoxic. PAN is the first compound of a homologous series whose phytotoxicity increases with molecular weight in the following sequence: peroxyacetyl nitrate (PAN) < peroxypropionyl nitrate (PPN) < peroxisobutyryl nitrate (PisoBN) < peroxybutyryl nitrate (PBN) < peroxybenzoyl nitrate (PBzN). Based on current knowledge none of these compounds, except PAN, occurs at phytotoxic concentrations in the atmosphere (Mudd, 1975; EPA, 1978a). The possible practical importance of the co-occurrence of PAN and ozone (Taylor, 1969; Temple, 1982) will be discussed as will the influence of the photochemical smog complex.

The basis for material selection, its organization, and presentation, was influenced by the relationships among ambient exposures, environmental factors, and plant responses (Figure 1) and the desire to provide a perspective for practical environmental protection measures in addition to reviewing available literature for students and researchers.

The reaction of a plant to a given air pollutant depends on the ambient exposure, the amount of pollutant diffusing into the leaves, and the plant's autonomous and environmentally controlled resistance. The degree of resistance is controlled primarily by the plant's genetic complement (4.3.2) and its developmental stage at the time of exposure (4.3.1) and, secondarily, by the modifying influence of various external factors (4.2). Depending on the intensity, nature, and frequency of the exposure (4.1), the developmental stage of the plant is influenced by given

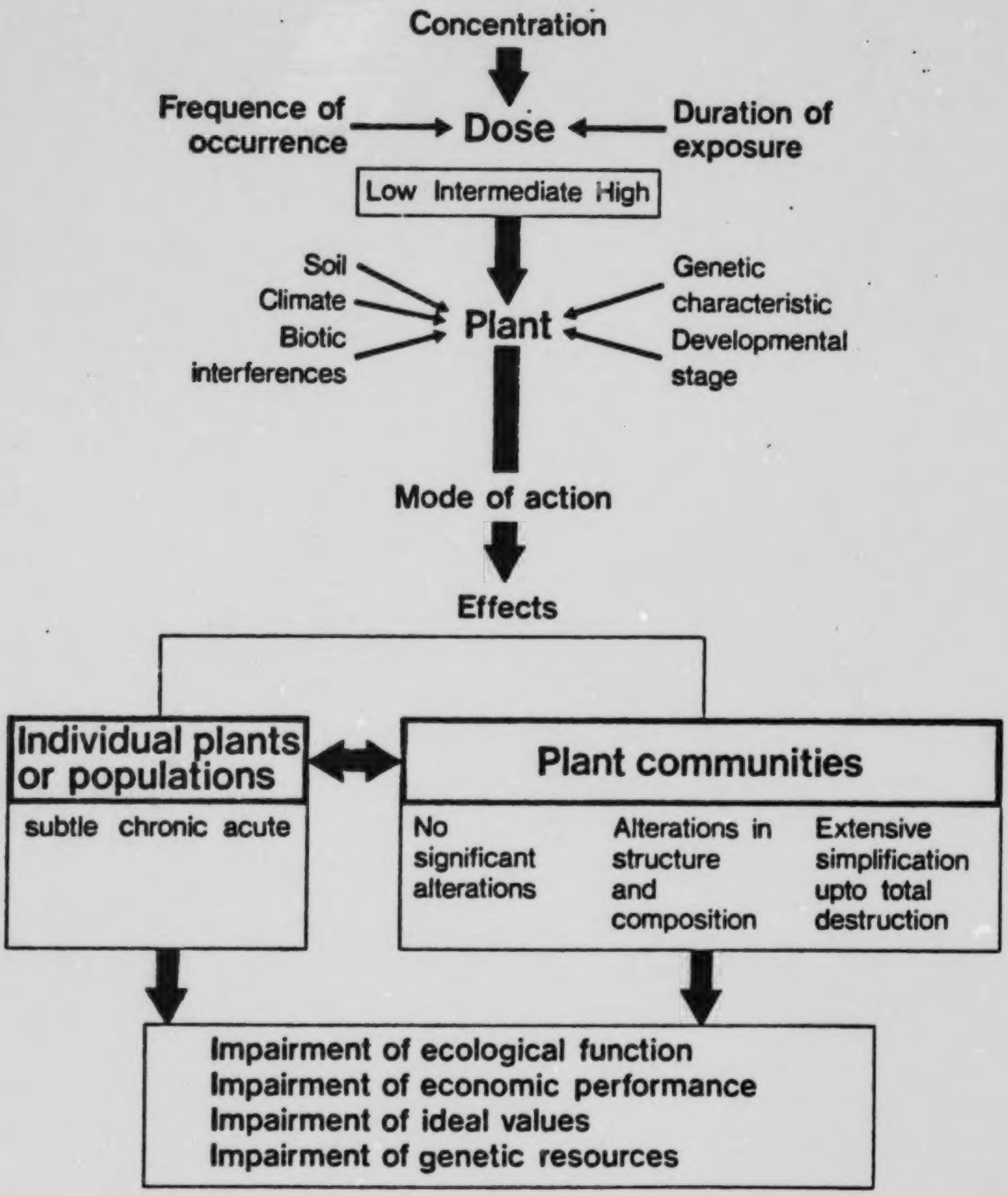
Concentration
Frequence of occurrence
Dose
Duration of exposure
Low Intermediate High
Soil
Climate
Biotic interferences
Plant
Genetic characteristic
Developmental stage
Mode of action
Effects
Individual plants or populations
subtle chronic acute
Plant communities
No significant alterations
Alterations in structure and composition
Extensive simplification upto total destruction
Impairment of ecological function
Impairment of economic performance
Impairment of ideal values
Impairment of genetic resources

Figure 1. Reactions of plants as individuals, populations, and communities to air pollutants, depending on various response-influencing factors.

environmental conditions such as climate (4.2.1), soil (4.2.2), and biotic factors (2.5). The response can range from acute, chronic (3.1.1), or subtle (3.1.2) injury on an individual plant to changes in plant communities, their composition, and structure (2.5). Injury to the ecological and economical functions of the affected plants can lead to an additional reduction in their ideal values and finally to gene erosion through the loss of species (3.3). A range of experimental and survey methods are available to determine the various air pollution effects at the individual organizational levels of the ecosystem (3.4).

Studies of air pollution effects on vegetation are not an end in themselves. Consequently, it is not sufficient to describe only the ambient exposure and resultant effects; a basis for remedial measures should be given. The implementation of these measures assumes that one has information about the type, intensity, spatial distribution, and cause of the pollution-induced injury. Presentations in Chapters 2 and 3 should help answer these questions, and also the extent that biological indicators can be used to detect and evaluate the risks arising from photochemical oxidants. The uses of, and possible changes in, plant cultural practices as a way to reduce effects of air pollutants on plants are discussed in Chapter 4.4.

The decisive factor in protecting vegetation is to reduce the ambient pollutant exposure. A significant basis for establishing air quality criteria is an accurate knowledge of the ambient exposure characteristics and the resulting responses. Data developed under various limiting conditions and from different countries were used to evaluate and interpret the quantitatively determined relationships between ambient exposure and effect, to derive the maximal acceptable ozone concentrations for the protection of vegetation (Chapter 6).

Photochemical oxidants constitute a complex mixture of secondary pollutants, many of which are biologically active and may co-occur with primary air pollutants. Therefore, the effects of the single gases and also pollutant combinations is discussed (Chapter 5). The evidence that ozone may be a primary cause of the new type of forest injury occurring in Central Europe is reviewed (Chapter 5.5). These topics, integrated with Chapter 2, "Mode of Action," provide a comprehensive analysis and description of pollution uptake and its effects on plants. A unique concept used to evaluate the results concerning the mode of action for ozone and PAN provides a significant basis for the recognition and evaluation of their effects in relation to practical environmental protection measures and for the formulation of additional research topics.

CHAPTER 2
MODE OF ACTION

The various plant responses to photochemical oxidants at various levels of biological organization are based on a sequence of biochemical and physiological events terminating in injury (Figure 2). From this perspective, Tingey and Taylor (1982) proposed a conceptual model to summarize plant responses which included pollutant uptake (leaf conductance), perturbation, homeostasis, and injury which can be equated with or lead into damage (see Chapter 3). This concept is summarized as a basis for discussing the mechanisms of ozone and PAN actions on vegetation.

Pollutant uptake is governed by leaf conductance (conductance = 1/diffusive resistance) which regulates pollutant movement from the ambient air into cellular perturbation sites. The gas phase movement of ozone into the leaf depends on the concentration gradient between the ambient air and sorptive sites within the leaf and the ease of mass transfer along the diffusive path. Following the sorption of pollutants onto the wet cell surfaces, their movement is controlled by liquid phase reactions, including diffusion and reaction with scavenging systems.

Perturbation is the initial phytotoxic event and results from ozone-induced alterations in cellular function or structure. The initial phytotoxicity is caused by the reactions of ozone or its derivatives with macromolecules that are active in cellular functions. The primary site for ozone reactions is cellular membranes causing changes in selective permeability.

Homeostasis is the recovery processes that occurs following perturbations. The cells may respond with either repair or compensatory mechanisms.

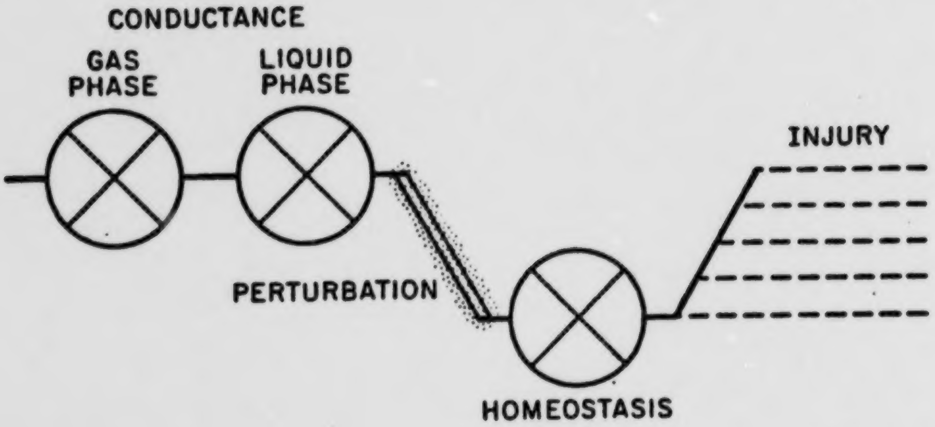
CONDUCTANCE
GAS PHASE
LIQUID PHASE
INJURY
PERTURBATION
HOMEOSTASIS

Figure 2. Conceptual model for the biochemical and physiological processes controlling plant response to ozone. The major processes controlling the response are leaf conductance (gas and liquid phases) and homeostasis (Tingey and Taylor, 1982).

Injury is caused by pollutant absorption and its subsequent reaction at active sites within the cell. Injury is the result of the inability to repair, or compensate for cellular dysfunctions. The primary role of membranes in metabolism and their reactivity with ozone suggests that metabolic repercussions will occur throughout the cell following membrane disruption.

2.1 Pollutant Uptake

Photochemical oxidants are absorbed directly from the atmosphere in contrast to some other air pollutants, for example, acidic gases and heavy metals which are absorbed both by the aboveground plant parts and the roots following deposition into the soil. Uptake is limited essentially to the chlorophyll-containing organs practically all the absorption occurs within the leaves. Gas absorption processes in leaves and plant canopies are described in the following sections.

2.1.1 Pollutant Uptake Into Leaves

Photochemical oxidant injury results from biochemical and physiological reactions occurring within the cells of the leaf interior. The rate and the amount of ozone and PAN that diffuse from the ambient air to reactive sites within the leaf area determinants of injury. Pollutant flux is a function of the chemical and physical properties along gas-to-liquid diffusive pathway. Physical structures may restrict pollutant flux; chemical reactions may scavenge ozone or PAN molecules within the gas and liquid phases.

2.1.1.1 Gas Phase Conductance

The absorption of gases, such as ozone or PAN, is the consequence of the chemical potential gradient between the bulk air (C_a) and the leaf interior (C_i). Flux is proportional to the pathway conductance (g) and inversely related to the resistances (R) to mass transfer along the diffusive pathway as the pollutant moves through the boundary layer (R_a), stomata and intercellular spaces (R_s), and the liquid phase (R_r). These relations have been used in many modeling studies of gas uptake (e.g., Bennett _et_ _al_., 1973; Ting and Dugger, 1968; Tingey and Taylor, 1982) and are illustrated in Figure 3. Total pollutant flux (J_{total}) is the sum of the flux to the leaf surface ($J_{surface}$) and the leaf interior ($J_{internal}$). Although both fluxes of photochemical oxidants may be large, cellular perturbations result only from gases diffusing into the leaves ($J_{internal}$). Because both the surface and internal fluxes may change during exposure, the ambient dose (concentration x duration of exposure) to which the plant is exposed is not necessarily a reliable estimate of the cellular dose that the plant actually receives.

The flux of the gases to the leaf surface is controlled by the boundary layer resistance (R_a), which is a function of leaf orientation, size, shape, epidermal characteristics, trichomes, and wind speed. The boundary layer thickness decreases with increasing wind speed and speeds above 2 m s^{-1} it can be neglected (Hill, 1971). However, in exposure chambers with low wind speeds or closed chambers with little or no air exchange, the boundary layer resistance can be appreciable and influence pollutant uptake. For example, ryegrass (Lolium perenne) exposed to SO_2 at a wind speed of 0.17 m s^{-1} was uninjured; when exposed at a wind speed of 0.42 m s^{-1} it displayed considerable injury (Ashenden and Mansfield, 1977).

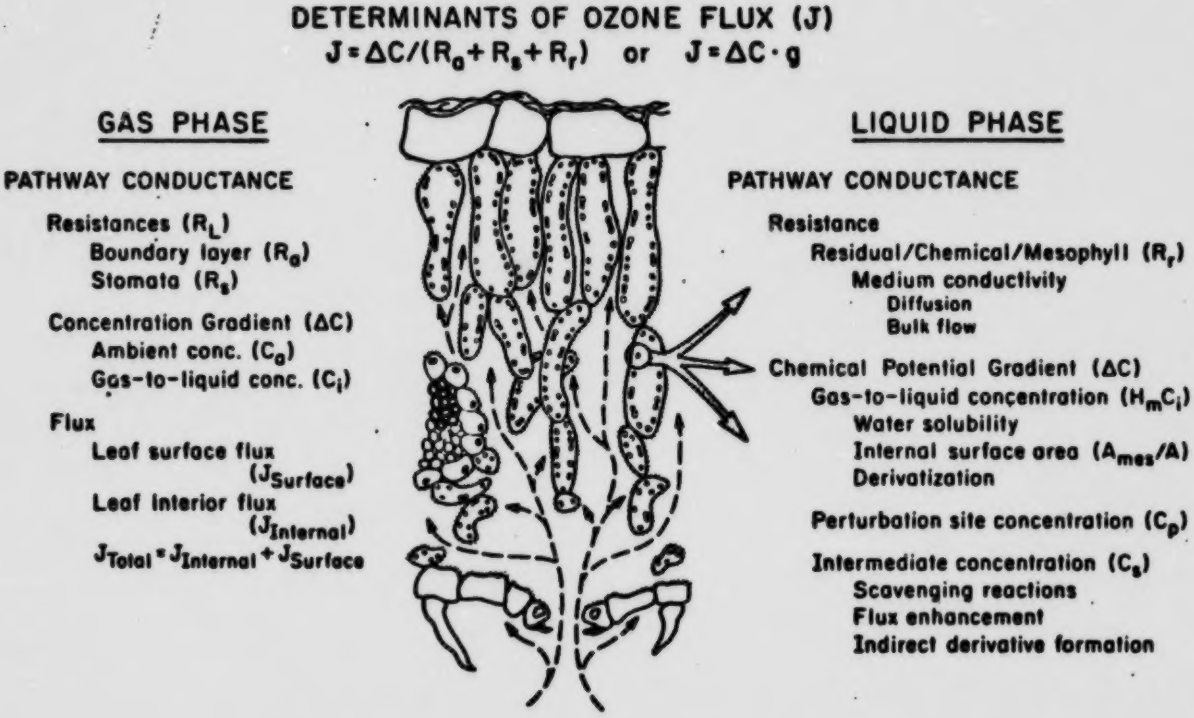
DETERMINANTS OF OZONE FLUX (J)
$J = \Delta C/(R_a + R_s + R_r)$ or $J = \Delta C \cdot g$
GAS PHASE
PATHWAY CONDUCTANCE
Resistances (R_L)
Boundary layer (R_a)
Stomata (R_s)
Concentration Gradient (ΔC)
Ambient conc. (C_a)
Gas-to-liquid conc. (C_i)
Flux
Leaf surface flux ($J_{Surface}$)
Leaf interior flux ($J_{Internal}$)
$J_{Total} = J_{Internal} + J_{Surface}$
LIQUID PHASE
PATHWAY CONDUCTANCE
Resistance
Residual/Chemical/Mesophyll (R_r)
Medium conductivity
Diffusion
Bulk flow
Chemical Potential Gradient (ΔC)
Gas-to-liquid concentration ($H_m C_i$)
Water solubility
Internal surface area (A_{mes}/A)
Derivatization
Perturbation site concentration (C_p)
Intermediate concentration (C_s)
Scavenging reactions
Flux enhancement
Indirect derivative formation

Figure 3. The relationship of pollutant flux, chemical potential gradient, and leaf resistances or conductances in the gas and liquid phases (Tingey and Taylor, 1982).

Similar results were obtained by Brennan and Leone (1968) in plant studies using ozone and SO_2. A sufficient air exchange and turbulence to minimize the boundary layer and prevent pollution depletion within the boundary layer are important considerations in establishing the comparability of results among experimental studies.

Leaf morphology can have a significant effect on pollutant flux. Elkiey _et_ _al_. (1979) related differential ozone resistance in petunia cultivars to trichome density, raised and roughened cuticular features, and small epidermal cells. They suggested that these morphological features influenced the amount of pollutant diffusing into the leaf. Bennett _et_ _al_. (1973) reported that pubescent leaf surfaces absorbed more ozone than glabrous ones.

In addition to the boundary layer resistance, stomatal resistance also influences pollutant uptake. Stomatal resistance is determined by stomatal number, size, anatomical characteristics of the guard cells and the size of the stomatal pore. There is general agreement that when the stomata are closed, pollutant uptake is reduced and essentially no plant injury results. The opening of the stomatal pore is controlled by the internal CO_2 concentration and the hydration of the guard cells; also it is influenced by temperature, relative humidity, light, plant nutrition, and water availability. The stomatal opening is controlled by the turgor differential between the guard cells and the adjacent subsidiary cells. When the guard cells have a higher turgor than the epidermal cells, the stomatal pores open; when it is less, the pore opening is reduced. The turgor differential results from the establishment of an osmotic gradient by the accumulation of K ions in the guard cells (Zelitch, 1969). The osmotically active K^+ causes an increased water absorption into the guard cells, increasing turgor.

The external and internal factors which directly or indirectly influence the stomatal control mechanisms alter the stomatal aperture, influencing pollutant uptake, as shown in Sections 4.2 and 4.3.

Numerous studies have focused on the association between stomatal resistance, ozone uptake, and the resultant foliar injury; most have concluded that stomatal resistance was the principal or sole factor controlling differential foliar injury (Table 1). This mechanism has been invoked to explain the differences in plant reactions to ozone as influenced by environmental factors -- edaphic and climatic, internal growth factors, and inter- and intraspecific differences in foliar sensitivity. The basic assumption is that pollutant uptake is proportional to stomatal resistance, therefore an increase in stomatal resistance will decrease internal ozone dose, reducing injury. However, experimental verification of this assumption is lacking (Table 1). The failure to measure ozone uptake to support this assumption may explain why injury is frequently not related to pollutant uptake.

However, other studies have not reported an association between stomatal resistance and foliar injury (Table 2). In some of these studies, ozone uptake was inferred from water flux data, but in others ozone flux was measured. It appears unwarranted to establish *a priori* a relationship between stomatal resistance and foliar injury.

The data relating ozone uptake to foliar injury are also contradictory. Ozone uptake was greater in young than old foliage of *Camellia* (Thorne and Hanson, 1972). Differences in total ozone flux were related to leaf-age response differences in tobacco (Craker and Starbuck, 1972).

Table 1. Examples of genetic and environmental control of ozone injury in which the mechanism was thought to be stomatal conductance. Ozone flux was not measured (Tingey and Taylor, 1982).

Genetic Variation	Environmental Variation
Interspecific	Edaphic
Pinus spp. (Evans and Miller, 1972b)	Potassium (Leone, 1976; Noland and Kozlowski, 1979)
Multiple spp. (Thorne and Hanson, 1972)	Water (Markowski and Grzesiak, 1974)
Intraspecific	Salinity (Hoffman *et al*., 1973, 1975)
Acer rubrum (Townsend and Dochinger, 1974)	Nitrogen (MacDowell, 1965a)
Nicotiana tabacum (Ting and Dugger, 1971; Dean, 1972; Rich and Turner, 1972; Turner *et al*., 1972)	Climatic Light (Dunning and Heck, 1973)
Allium cepa (Engle and Gabelman, 1966)	Humidity (Otto and Daines, 1969)
Phaseolus vulgaris (Thorne and Hanson, 1976; Butler and Tibbits, 1979b)	Atmospheric Ozone dose (MacDowall, 1965a; Hill and Littlefield, 1969; Runeckles and Rosen, 1977)
Developmental	Abscisic acid (Fletcher *et al*., 1972)
Hypericum spp. (Ledbetter *et al*., 1959)	Other pollutants (Jacobson and Colavito, 1976)
Nicotiana tabacum (Glater *et al*., 1962)	

Table 2. Examples of variable plant responses to ozone that are not associated with differential gas phase conductance (Tingey and Taylor, 1982).

	Flux Measurement		
Variation Source	Water Vapor	Ozone	Reference
Genetic			
Interspecific			
Cucumis sativus	X		Beckerson and Hofstra, 1979a
Raphanus sativus			
Glycine max			
Multiple Species		X	Townsend, 1974
Intraspecific			
Vitis labrusa	X		Rosen *et al*., 1978
Glycine max		X	Taylor *et al*., 1982
Developmental			
Phaseolus vulgaris	X		Evans and Ting, 1974a
Nicotiana tabacum		X	Leuning *et al*., 1979b
Gossypium hirsutum	X		Ting and Dugger, 1968
Glycine max		X	Taylor *et al*., 1982
Environmental			
Biotic			
Nicotiana tabacum virus	X		Brennan, 1975
Glycine max virus	X		Vargo *et al*., 1978
Atmospheric			
Ethylene diurea chemical *Phaseolus vulgaris*	X		Carnahan *et al*., 1978

However, there was no consistent pattern between ozone uptake and the sensitivity of nine shade tree species to ozone (Townsend, 1974). Ozone flux for two sensitive species, Fraxinus americana and Quercus alba, ranged from 398 to 1,058 μg m^{-2} s^{-1}, respectively.

If ozone injury is dependent solely on internal ozone flux, then internal flux should be a reliable predictor of foliar injury. In Petunia hybrida cultivars, the sensitive cultivar absorbed significantly more ozone than the resistant one (Elkiey and Ormrod, 1980a). However, differential sensitivity in soybean cultivars was not associated with the internal pollutant flux (Taylor et al., 1982). The sensitive cultivar consistently absorbed less ozone than the resistant cultivar. Ozone uptake per cell has been estimated for several plant species (Craker and Starbuck, 1973; Heath, 1975; Taylor et al., 1982). Based upon these studies, injury thresholds appear to be 20 to 40 fmoles/cell.

The stomatal conductance of bean leves expose to subinjurious levels of PAN was similar to the controls (Metzler and Pell, 1980). Following exposure to injurious levels, stomatal conductance was higher in the dark and lower in the light than in control plants, suggesting that the injury reduced the diurnal amplitude of leaf resistance. The relationship with the stomata was correlated with the appearance of cellular injury.

2.1.1.2 Liquid Phase Conductance

The diffusion of ozone from extracellular deposition sites to cellular perturbation sites includes movement through the liquid phase of the cell. Along this pathway it may experience diffusion, and/or bulk flow through hydrated cell walls, membranes, and cytosol, each of which is more viscous than air. Therefore, diffusion will proceed several orders of magnitude slower than for equivalent distances in air. Also, the transfer of ozone may be impeded by scavenger reactions that consume ozone. This chemical reactivity in the liquid phase may affect ozone movement, i.e., potential gradient and distribution within the cells. In solution, unsaturated fatty acids, sulfhydryl, and ring-containing compounds are ozone-susceptible. The reaction of ozone with olefinic double bonds produces an aldehyde or ketone and a Criegee zwitterion which decomposes to produce another aldehyde or ketone and hydrogen peroxide (Tingey and Taylor, 1982). Ozone has also been shown to increase free radicals in plant leaves indirectly or by decomposition in solution (Tingey and Taylor, 1982). Biological systems have evolved scavenging or buffering systems such as superoxide dismutase, catalase, or peroxidases to metabolize free radicals (McCord et al., 1971; Fridovich 1975, 1978). The importance of oxidant-scavenging processes in aerobic metabolism (Fridovich, 1975, 1978) suggests that these processes would be important in controlling ozone distribution within the cell. Foliar or root applications of an ethylene diurea (EDU) prevented foliar injury (Carnahan et al., 1978; Lee and Bennett, 1982) without affecting pollutant uptake (Bennett et al., 1978). The EDU-induced resistance was associated with higher tissue levels of superoxide dismutase and catalase (Lee and Bennett, 1982). Young leaves of Populus euramericana are more resistant to sulfur dioxide and contain higher superoxide dismutase activity than older leaves (Tanaka and Sugahara, 1980). Similarly, the higher ozone resistance of young bean leaves compared to older ones has been associated with higher superoxide dismutase levels (Lee and Bennett, 1982).

Other scavenging mechanisms have also been suggested. Giese and Christensen (1954) proposed that the cell's first defense against ozone was reactive organic matter on the cell surface coat. The variable ozone response of cell cultures of Saccharomyces cerevisiae was related to an array of unspecified intracellular scavenger molecules (Dubeau and Chung, 1979). Sulfhydryls (e.g., glutathione), sulfhydryl proteins, cysteine, and small amounts of methionine apparently serve as free-radical scavengers and peroxide decomposers (Tingey and Taylor, 1982).

2.1.2 Pollutant Uptake by Plant Canopies

Gas uptake by plant canopies is controlled by the same general processes (concentration gradient, and resistance to mass transfer) that control diffusion into leaves. Only the magnitude of the parameters and some of the physical impediments are changed. Pollutant uptake by alfalfa canopies has been measured in both gas exchange chambers and in field studies (Hill, 1971). Given constant environmental conditions, pollutant uptake by alfalfa was proportional to pollutant concentration. However, at higher ozone concentrations, stomatal closure occurred, causing a proportional reduction in ozone uptake.

Using a wind tunnel, Garland and Penkett (1976) estimated sorption rate of PAN to a grass stand, suggesting a deposition velocity of 0.25 cm s^{-1}. However, this value did not consider the influence of internal and external factors on the pollutant uptake rate.

Treshow and Stewart (1973) measured ozone concentrations of 0.09 ppm above an aspen canopy and 0.01 ppm within the canopy, indicating a significant sorption by the canopy. This concentration differential was maintained even at wind velocities up to 9 m s^{-1}. Using micrometeorological techniques, ozone uptake has been measured for corn and tobacco fields

(Leuning _et_ _al_., 1979a, 1979b; Weseley _et_ _al_., 1978). Uptake rate range from 1.1 to 9.0 nmoles cm^{-2} h^{-1}.

2.2 Perturbation

Probable sites of ozone-induced perturbations are those highly ordered molecular configurations that are essential to the function of the cell. Experimental results, primarily from ultrastructural and biochemical studies, suggest that the membranes are the primary site of ozone action. Initial ultrastructural changes are diverse, but most indicate membrane dysfunction (see Section 2.4.1). Tobacco plants exposed to ozone (0.18 ppm) exhibited a loss of turgor within a few minutes after the exposure started indicating an increase in membrane permeability (Keitel and Arndt, 1983). Subsequently, photosynthesis and transpiration were reduced. These obsevations support the theory that the primary effect of ozone is to increase the permeability of the plasmalemma causing ionic imbalances which are reflected in altered metabolic processes.

Various indicators of membrane permeability have been proposed as measures of ozone perturbations at the cellular level (Heath, 1975). Many studies have shown the effects of ozone on plant membranes. For example, ozone exposure to citrus and bean leaves doubled their permeability to radioactive glucose (Dugger and Palmer, 1969; Percherowicz and Ting, 1974). Also, there was an increased loss of ^{86}Rb (Evans and Ting, 1973); K^+ loss was increased and uptake was reduced (Heath _et_ _al_., 1974; Chimiklis and Heath, 1975; Heath and Frederick, 1979). The effects were reversible following short term exposures, but continued ozonation caused irreparable injury to membrane components. These data suggest an effect at a limited number of transport sites rather than a general deterioration of the membrane. Alterations in membrane integrity may cause spatial dislocations of membrane components affecting metabolic processes such as photosynthesis. Ozone effects on photosynthesis have been associated with an impairment of membrane-bound systems (Chang and Heggestad, 1974; Koiwai and Kisaki, 1976). Coulson and Heath (1974) concluded that "... ozone disrupts the normal pathway of energy flow from light-excited chlorophyll into the photoacts by the disruption of the components of the membrane but not a general disintegration of the membrane."

The effects of ozone on various chemical components of membranes have been studied in both artificial systems and intact membranes. The lipid component of cellular membranes is ozone labile, with the olefinic double bonds of the unsaturated fatty acids being oxidized to form shorter chain saturated carboxcylic acids, aldehydes, and a few other reaction products (Teige et al., 1974; Goldstein, 1977; Mudd, 1982). However, these results from isolated systems have not been confirmed in most vegetation studies. Tomlinson and Rich (1969b) observed a reduction in the fatty acid of tobacco leaves following exposure. In contrast, Swanson et al. (1973) found that some fatty acids were decreased but others increased. Mudd (1982) has concluded that "Although the reaction of ozone with unsaturated lipids as a basis for ozone toxicity is intellectually appealing, the body of evidence does not clearly support such a hypothesis."

Ozone can oxidize free amino acids with the most susceptible being: cysteine, tryptophane, methionine and, to a lesser extent, histidine and tyrosine (Mudd, 1982). Although the oxidation of free amino acids can have harmful consequences, the reaction of ozone with susceptible amino acid residues in various proteins would have serious metabolic effects for the cell, depending on the enzyme turnover rate. The sensitivity of various proteins to ozone and identification of the labile amino acid residues have been reviewed (Mudd, 1982). Sulfhydryls also are oxidized by ozone to disulfides and sulphonates (Tomlinson and Rich, 1970; Mudd, 1982). Thiol compounds are oxidized by PAN (Mudd, 1982). Sulfhydryl compounds are part of the active site of several enzymes and contribute to the tertiary structure of the various proteins. The effects of ozone and PAN on the protein constituents of membranes will have important consequences for normal membrane function.

2.3 Homeostasis

Following a perturbation, living cells attempt to reestablish their normal metabolic levels using repair and/or compensatory processes (Levitt, 1980). By definition, repair processes correct the perturbation, eliminating the dysfunction. In compensation, the perturbation and its physiological consequences remain but the cells react with processes that counter the detrimental effects of the perturbation. Because repair and compensation may range from partial to complete, injury will vary as well.

Mudd (1980) suggested that resistant plants possessed a greater capacity of unspecified mechanisms that repaired cellular injury. In microscope studies of pollution-impacted spruce needles, Sorauer and Ramann (1899) observed the repair of cellular dysfunction. On dicotyledonous plants, an early symptom of ozone injury is the appearance of water-soaked (shiny or oily) areas on the leaf surface which result from an increased membrane permeability and cell contents leaking into the intercellular spaces. In resistant plants this symptom may be temporary, while in sensitive plants it can develop into necrosis. In beans, leaf age variability in ozone susceptibility was attributed to variation in energy pools which governed the repair rate (Dugger et al., 1962b). Ozone elevated potassium in Chlorella; however, within 2-3 min after ozonation stopped, the normal efflux rate was reestablished (Heath et al., 1974). The time required to reestablish the normal potassium efflux rate decreased with increasing temperature (Chimiklis and Heath, 1975).

Ozone increased membrane permeability to glucose and 2-deoxy-glucose (Perchorowicz and Ting, 1974) which have been used as indicators of membrane permeability and repair (Sutton and Ting, 1977a, 1977b). Continuous light or glucose additions enhanced membrane repair, while low temperatures or darkness retarded it (Sutton and Ting, 1977a, 1977b). These observations support the concept that the repair of altered membrane permeability is energy-dependent.

The hexose monophosphate shunt provides reducing power (NADPH) which may be used, in part, to reduce disulfides and peroxides (Mudd and Freeman, 1977; Freeman et al., 1979) and supply biosynthetic reductant. Ozone increased the activity of glucose-6-phosphate dehydrogenase in soybean cultivars within 3-6 h following an ozone exposure and it remained elevated for several days (Tingey et al., 1975, 1976a). Sutton and Ting (1977a, 1977b) concluded that an endogenous energy source was "... needed for the reestablishment of the important membrane sulfhydryls and unsaturated lipids oxidized by ozone so that normal transport and permeability are restored to the cell membrane."

2.4 Injury

Injury results from the inability to repair or compensate photochemical oxidant-induced perturbations. Biochemically, injury is expressed as alterations in metabolism, including enzyme activities and metabolite pools. These cellular disturbance can also be expressed cumulatively as foliar pathologies, altered carbohydrate allocation, reduced growth and yield, and impacts on plant communities and ecosystems. These ozone responses (i.e., altered metabolism) are the consequences of pollutant-induced perturbations rather than the primary effect of ozone.

Changes in metabolism result from alterations in the structure and function of specific membrane components. The increased membrane permeability is associated with increased water and ion losses and partial loss of cellular compartmentalization, resulting in altered metabolic processes (Tomlinson and Rich, 1967; Howell, 1974; Tingey et al., 1975). The numerous biochemical and physiological reactions that have been correlated with photochemical oxidant impacts are only partially specific for oxidants. Most reactions may also be induced by other pollutants and various environmental stresses (Levitt, 1980).

2.4 Ultrastructural Changes

The development of visible foliar injury symptoms results from biochemical and physiological changes. These changes include both functional and structural characteristics resulting from disruption of cellular membranes (see 2.2). Foliar injury is the consequence of biochemical and ultrastructural changes which have been established in some detail for injurious oxidant effects (Thomson, 1975). The first identifiable ultrastructural changes occur within the chloroplast (Thompson et al., 1966), not the plasmalemma.

Thomson et al. (1966) observed an increased granulation and electron density of the chloroplast stroma following the exposure of bean leaves to ozone (0.6 to 1.0 ppm for 30 min). Crystalline fibril arrays composed of fibers approximately 85 nm in diameter were formed during the exposures, similar to the fibrils induced in bean plants exposed to PAN (Thomson et al., 1965). Similar fibrils were reported by Thomson and Swanson (1972) following treatment of cotton (Gossypium hirsutum) leaves with ozone. The crystalline fibril arrays were not observed in tobacco leaves, but indentation of the outer chloroplast membrane such as that reported for bean leaves (Thomson et al., 1966). Membrane indenting can co-occur with the crystalline arrays (Thomson et al., 1974) and can be induced by other polluants, e.g., NO_2 (Dolzman and Ullrich, 1966; Thomson, 1975). De Greef and Verbelen (1973) showed that various stresses such as mineral deficiency, mechanical injury, or water stress induced the crystalloids, with water stress the primary cause. The crystalline fibrils were observed in isolated chloroplasts suspended in a hypotonic medium (Perner, 1962, 1963; Shumway et al., 1967), in the chloroplasts from wilted leaves, or from plasmolyzed leaf cells (Wrischer, 1973). Dehydration could also be the primary cause of photochemical oxidant-induced fibril formation as a consequence of the permeability changes in the plasmalemma and chloroplast membranes following exposure. As stated above, these changes occur in the chloroplasts prior to observable ultrastructural changes in the plasmalemma, which shows modifications only after other fine structure changes. These data led Swanson et al. (1973) to question the hypothesis that the plasmalemma was the primary site of ozone attack. Other data also suggest that the plasmalemma may not be the primary site of ozone reactions. Using data from red blood cells, Mudd (1982) provided evidence to suggest that ozone or a derivative may diffuse through membranes. To explain the observations of structural changes in the chloroplasts prior to changes in the plasmalemma, Tingey and Taylor (1982) proposed that ozone indirectly induced free radical formation in chloroplasts. Water and ion loss from oxidant-injured cells are not necessarily related to structural changes in the plasmalemma but represent biochemical disruptions of the membrane, as shown in Section 2.2. In addition, there is a series of secondary effects that are difficult to explain without membrane injury.

Because the enzymes of photosynthesis are located in the chloroplast, it is obvious that ultrastructural changes in the chloroplast could readily inhibit photosynthesis. The increased electron density in the chloroplast stroma, formation of crystalloids, and rupturing of the outer chloroplast membrane are the first fine structural changes observable from acute oxidant exposure. In morning glory leaves exposed to ozone (0.15 ppm for 8-h), there was a reduction in chloroplast size, disintegration of the thylakoids, and a decrease in ribosomes (Toyama, 1976). Plastoglobules and phytoferritin increased in the chloroplasts and there was swelling in the cristae of the mitochrondria. With time, the chloroplast and mitochondria swelled (Lee, 1968; Swanson et al., 1973). The electron density of the cytoplasm increased, the plasmalemma withdrew from the cell wall and the cellular organelles congregated in the cell center. The vacuole ruptured and the remaining organelles were destroyed; the cell contents collapsed into a thick mass and only the granal membranes and crystalline fibrils were recognizable (Thomson et al., 1966; Thomson et al., 1974; Thomson, 1975). There are deviations from this general scheme, depending on plant species, leaf age, and oxidant dose (Mitchell et al., 1979; Pell and Weissberger, 1976). An 8-h PAN exposure (0.15 ppm) also induced swelling in the mitochondria (Toyama, 1976).

Ultrastructural changes induced by moderate short-term ozone exposures may be reversible (Athanassious, 1980): invagination of the chloroplast lamellae, granulation, and increased electron density in the stroma were no longer observable several hours following ozone treatment. These responses are typical of water deficiency (Shumway et al., 1967) and are symptomatic of indirect ozone effects on the organelles (Pell and Weissberger, 1976). At higher ozone concentrations, the cell membranes -- the tonoplast, plasmalemma, and endoplasmic reticulum -- are destroyed, leading to cell death (Athanassious, 1980; Pell and Weissberger, 1976). Petunia pollen exposed to ozone also displayed fine structure changes. The organelles were withdrawn from the plasmalemma and congregated in the cell center, as occurred in mesophyll cells (Harrison and Feder, 1974). The biochemical, physiological, and ultrastructural changes in the cell (Chapter 2) lead to histological and anatomical injury expressions (Chapter 3).

2.4.2 Nitrogen Metabolism

Free amino acids increased in the foliage of several plant species following ozone exposure (Tomlinson and Rich, 1967; Howell, 1970; Ting and Mukerji, 1971; Craker and Starbuck, 1972; Mumford et al., 1972; Tingey et al., 1973a). An impairment in protein synthesis may be inferred from the ozone-induced dissociation of polysomes (Chang, 1971a, 1971b). However, effects on foliar protein contents are less clear with protein decreases, increases and no effects being reported (Ting and Mukerji, 1971; Craker and Starbuck, 1972; Beckerson and Hofstra, 1979c; Tingey et al., 1973c).

2.4.3 Carbohydrate Metabolism

Following the observation that PAN reduced the elongation of oat coleoptiles (Ordin, 1962), it was shown that ozone and PAN inhibited the enzymes involved in cell wall biosynthesis, both in vitro and in exposed seedlings (Ordin and Hall, 1967; Ordin et al., 1967, 1969; Gordon and Ordin, 1972). PAN-exposed tobacco leaves yielded similar results except that the activity of phosphoglucomutase was unaffected and the activity of UDP-glucose-pyrophosphorylase was doubled (Ordin et al., 1971). This increased enzyme activity was associated with PAN-induced membrane disruptions releasing bound enzymes.

Immediately following ozone exposure, soluble sugars in soybean leaves and pine needles decreased (Tingey et al., 1973c; Wilkinson and Barnes, 1973). Subsequently they increased, frequently in association with foliar injury (Bennett et al., 1977; Tingey et al., 1973a; Miller et al., 1969; Barnes, 1972b; Dugger et al., 1962a, 1966). The increase in soluble sugars could result from reduced translocation or inhibition of starch synthesis. Acute exposures reportedly reduce starch content (Dugger et al., 1962a; Youngner and Nudge, 1980). The increase in soluble sugars and decrease in starch was also observed following chronic exposures (Miller et al., 1969; Dugger and Palmer, 1969).

2.4.4 Stress Metabolism

Ethylene is an important plant metabolite whose production is stimulated by ozone and other stresses (Craker, 1971a; Abeles and Abeles, 1972; Tingey et al., 1976b; Stan et al., 1981). This stress ethylene precedes the appearance of visual injury; it increases proportionally to the applied stress and its production has been associated with many of the ozone response symptoms, including ozone-enhanced leaf abscission and the formation of pigment systems characteristic of ozone injury. The activities of phenylalanine ammonia lyase, polyphenol oxidase, and peroxidases are stimulated by ozone exposure prior to the appearance of visual symptoms and remain elevated for several days (Tingey *et al.*, 1975, 1976a; Curtis *et al.*, 1976). These enzymes are involved in phenol biosynthesis and oxidation. An ozone-induced accumulation of phenols has been reported in many plant species and associated with the extent of foliar injury (Howell and Kremer, 1973; Howell, 1970; Howell, 1974; Koukol and Dugger, 1967; Tingey *et al.*, 1976a). Howell and Kremer (1973) identified the pigments formed in ozone injured leaves as polymerized phenols, proteins, and amino acids. They suggested that ozone induced cellular changes that either allowed more oxygen to enter the cells or oxidative enzymes to react with phenols, forming quinones that polymerized with protein and amino acids, yielding the pigments seen in ozone injury.

2.4.5 Photosynthesis

Numerous reports have described the effects of ozone and PAN *in vivo* and *in vitro* on individual photosynthetic processes. The following discussion illustrates that photosynthesis has numerous sites susceptible to photochemical oxidants.

When isolated chloroplasts were exposed to PAN (0.6 ppm for 0.5 h), oxygen evolution was reduced, but photophosphorylation was unaffected. At higher PAN concentrations, especially when illuminated during exposure, photophosphorylation was inhibited (Dugger *et al.*, 1965). The sulfhydryl reagent N-ethylmalimid inhibited photophosphorylation only in the light (McCarty *et al.*, 1972), suggesting an association between illumination and the presence of reactive sulfhydryl compounds. The redox system of photosystem II was oxidized (Dugger and Ting, 1968). Photosystem II also is sensitive to disruption by ozone (Chang and Heggestad, 1974; Koiwai and Kisaki, 1976). Coulson and Heath (1974, 1975) proposed that ozone and PAN inhibited photosynthesis by different mechanisms. Ozone attacked chloroplast membranes, disrupting the membrane-bound process of photosynthesis. In contrast, PAN diffused into the chloroplast which in the light was alkaline, causing the decomposition of the PAN where its reaction products could attack the sulfhydryl groups of the membranes and ribulose-1,5-biphosphate (RuBP) carboxylase inhibiting photosynthesis. Ozone also reduced the activity of the carboxylase, decreasing CO_2 fixation (Nakamura and Saka, 1978). Inhibition of RuBP carboxylase activity occurs shortly after ozone exposure. Pell and Pearson (1983) reported decreases of 36, 68, and 80%, respectively, in RuBP carboxylase activity in the foliage of three alfalfa cultivars 48-h following ozone exposure. These decreases occurred in the absence of visible injury. Coyne and Bingham (1981) found that the photosynthetic rate of field-grown ponderosa pine trees exposed to ambient photochemical oxidants was depressed to a greater extent than could be explained by stomatal closure; they suggested an impairment of excitation or carboxylation reactions. Several enzymatic processes of the Calvin cycle and the C_4-dicarboxcylic acid cycle are activated by light and sulfhydryl compounds (Mudd, 1975; Anderson et al., 1974). Photochemical oxidant reactions with these sulfhydryl groups would reduce the secondary reactions of photosynthesis.

Ozone in high concentrations for a short time can destroy chlorophyll, leading to a reduced photosynthetic rate. Chlorophyll loss following ozone exposure has been reported in many species (e.g., Adedipe et al., 1973a; Miller et al., 1963; Runeckles and Resh, 1975a; Knudson et al., 1977). Chlorophyll b was more susceptible than chlorophyll a to ozone inactivation (DeKoning and Jegier, 1968b); Kühl and Wagner, 1970; Nobel, 1974); however, Verkroost (1974) found that chlorophyll a was more sensitive. Carotenoids were more susceptible to PAN than chlorophyll (Dugger _et al_., 1963a) but chlorophyll _a_ was more susceptible than chlorophyll _b_ (Gross and Dugger, 1969).

Carbon dioxide fixation was reduced following short-term exposures to acute-injurious concentrations of ozone (Todd, 1958a; Todd and Probst, 1963; Barnes, 1972a; Furukawa and Kadota, 1975). This reduction results from ozone-induced stomatal closure and inhibition of the enzymes of photosynthesis (MacDowall, 1965b; Hill and Littlefield, 1969). Numerous studies have shown that the net photosynthetic rate was reduced shortly after the start of the ozone exposure; when the exposures were terminated, the net photosynthetic rate rapidly returned to its original level (Hill and Littlefield, 1969; Pell and Brennan, 1973). The impact of ozone on photosynthesis was influenced by the season of year and the oxidant resistance of the test plants (Lorenc-Plucinska, 1979). Net photosynthesis can be impaired without the development of visible symptoms (Hill and Littlefield, 1969; Botkin _et al_., 1972), however, the appearance of visible symptoms is always associated with a measurable reduction in photosynthesis (Pell and Brennan, 1973).

Ponderosa pine trees were exposed to 0.15 ppm ozone for 30 days without the development of visible symptoms, but the net photosynthesis was reduced 10% compared to the controls (Miller _et al_., 1969). Similar results were reported for citrus trees grown in field conditions receiving polluted air (Thompson _et al_., 1967); the photosynthetic rate was reduced in the absence of visible injury when compared to trees grown in filtered air. Under chronic exposures, ozone caused a reduction in soluble sugars and starch (Miller _et al_., 1969; Tingey, 1974; Tingey _et al_., 1976a), leading to reduced growth (Jensen, 1981a) and yield (see Section 2.5).

Associated with reduced photosynthate production there is an alteration in the partitioning of photosynthate, reducing root growth and root processes which restrict shoot growth (Manning _et_ _al_. 1971; Tingey, 1974; Tingey _et_ _al_., 1976c; Oshima _et_ _al_., 1978; Blum and Tingey, 1977). Ponderosa pine seedlings exposed to 0.1 ppm ozone 6 h/day during the growing season had lower root reserves of soluble sugars and starch in autumn (Tingey _et_ _al_., 1976c), so that the plants had a diminished carbohydrate reserve for initial growth the following spring.

2.4.6 Respiration

Respiration was increased following short-term exposures to ozone and PAN. In bean leaves, there was a significant increase in respiration after exposure to 4.0 ppm ozone for 40 min; the increase paralleled the development of visible symptoms and then decreased (Todd, 1958a). Immediately following a 1-h ozone exposure of tobacco leaves, respiration initially decreased, then increased (MacDowall, 1965b). Following long-term exposures at 0.15 to 0.25 ppm for 5 days, the respiration rate of citrus leaves was increased (Dugger and Palmer, 1969). The ozone-induced alterations in foliar metabolic processes also influence root reactions. The root respiration of bean plants was reduced following 3-h exposures to 0.15 ppm ozone (Hofstra _et_ _al_., 1981).

2.4.7 Senescence

Particularly following chronic oxidant impacts, there have been numerous associations made between subtle injury reactions and premature senescence, which is characterized by increases in catabolic reactions and decreased anabolic reactions. These catabolic reactions include loss of starch (Dugger and Palmer, 1969; Youngner and Nudge, 1980), proteins (Craker and Starbuck, 1972), and chlorophyll (Adedipe et al., 1973a; Runeckles and Resh, 1975a), and increases in anthocyanins and polyphenols (Koukol and Dugger, 1967; Howell, 1970, 1974; Kremer and Howell, 1974). Also, there is a decrease in RNA content current with an increase in RNase activity (Craker and Starbuck, 1972), increases in peroxidases (Dass and Weaver, 1972; Flueckiger et al., 1979; Endress et al., 1980), respiration (Pell and Brennan, 1973), and stress ethylene production (Abeles and Abeles, 1972; Tingey et al., 1976b; Flueckiger et al., 1979; Stan et al., 1981). Premature leaf abscission (Jensen, 1973; Miller et al., 1969, 1977; Flueckiger et al., 1979; Williams, 1980) and fruit drop (Thompson and Taylor, 1969; Thompson et al., 1972) also occur.

These reactions and others discussed in the injury section can affect the magnitude of oxidant impact on plant growth and yield (see 2.5, 3.3) if specific thresholds are exceeded. In addition, for useful plants these reactions can, in part, influence plant quality. Pollutant-stressed plants may be more susceptible to biotic and abiotic stresses (Section 2.5).

2.5 Effects on Plant Communities and Ecosystems

In the preceding sections, the effects of photochemical oxidants focused on impacts on individual plants and homotypic populations. The responses of higher plant communities have received only limited study. The most important results of this research will be presented. With the increasing significance of photochemical oxidants in all industrial areas and the continuing widespread distribution, indications are that ecosystems even in remote areas will be impacted.

2.5.1 Reactions of Plant Communities Related to Air Pollutant Concentrations

As with individual plants, the responses of plant communities and ecosystems depend on pollutant dose. Based on the presentation of Smith (1974), Guderian and Küppers (1980b) analyzed air pollution effects on plant communities; in general, their scheme (Figure 4) is followed in this section.

2.5.1.1 High Pollution Dosage

A characteristic of the association between high dosage and plant community response is a breakdown of community structure, which is more or less obvious depending on ecosystem complexity. The degradation of the system is characterized by a rapid change in structure accompanied by and finally replaced by, secondary succession processes that under continuing exposure lead to a new equilibrium.

In forest ecosystems, the direct effects (acute and chronic) are observed first on the most sensitive tree species. In high pollution-impacted areas of southern California, 24% of the trees died within a 4-year period (Cobb and Stark, 1970; Miller, 1973a; Taylor, 1973b). The forested area around Crestline in the San Bernardino National Forest, California, is dominated by the oxidant-sensitive Jeffrey pine (Pinus jeffreyi). In 1969, in a study area of 64380 ha, intense, moderate, and no visible effects were found on 18492, 21568, and 24320 ha, respectively. Approximately 1.3 million individual trees were affected: 82% moderate, 15% intense injury, and 3% dead (Wert _et_ _al_., 1970).

In oxidant-injured forests, the amount of dead wood is increased through enhanced morbidity and mortality. This dead material is a significant source of fuel for forest fires. Thus, while fires in injured forests may not occur more frequently, they are more intense, producing higher temperatures. These higher temperatures cause more injury to soil organisms and to sensitive plant organs in the soil (Taylor, 1973a).

When pollutant impacts open the crowns of sensitive trees, air pollution can penetrate deeper into the stand and successively destroy the shrub, herb, and moss layers. Such complete vegetation destruction has been observed in the vicinity of individual sources emitting high concentrations of phytotoxic compounds (Niklfeld, 1967; Guderian and Stratmann, 1968; Hajduk and Ruzicka, 1969; Brandt and Rhoads, 1972). There are no reports of such intense damage resulting from photochemical oxidant exposure. However, under high pollution exposure, the elimination of sensitive species may have far-reaching consequences for the total ecosystem: previously the dense stands would protect the shrubs and herb layers, but as they are impacted the sensitive species will disappear. At least 10 shrub species in the shrub layer of the coniferous forests of the San Bernardino Forest are now endangered by this means (Cobb and Stark, 1970). It is no longer possible to determine how many species have disappeared during the last 20 years of pollution impacts.

Concurrent with the degradation of the original vegetation, secondary succession processes are initiated: pollution-resistant species whose ecological amplitude corresponds with the biotic and abiotic conditions immigrate and, with the remaining pollutant-stressed species, develop a newly structured ecosystem of less complexity. As is typical of ecotones, few species with high abundance occur in agreement with the second biocoenotypic principal. Wolak (1971) has described such a secondary plant community (industriogenous) resulting from continuing exposure to sulfur dioxide, zinc, and lead in the Upper Silesian district of Poland and named it the Industrial Climax Community. These ecosystems are characterized by reduced diversity, reduced productivity, and possibly reduced stability.

2.5.1.2 Intermediate Pollution Dosage

Intermediate air pollution dosages are ecologically and economically significant because their chronic and subtle, direct and indirect effects on individual species can set the stage for changes in community structure and function. Immediate, direct damage (i.e., primary injury) is the most common under high dosages, while under intermediate and low dosages the secondary effects such as reduced vigor including increased susceptibility to abiotic and biotic stresses (Wentzel, 1965; Donaubauer, 1966; Heagle, 1973; Huttunen, 1980; Laurence, 1981) become more significant. At moderate doses, primary and secondary injury lead to disruptions in growth, reproduction, and vigor of the more sensitive plant species within the community. Resistant species may display a higher productivity based on more favorable competitive conditions (Miller and Kickert, 1980) and attain a higher dominance within the plant community (Harward and Treshow, 1971).

In productive ecosystems, decreased yield resulting from reduced plant productivity can be reliably identified and evaluated. However, the conditions necessary to determine pollution-induced reductions in the ecological performance of plants and plant communities are generally insufficient. Therefore, in the highly structured forest communities with their delicate equilibrium with regard to plant strata, small decreases in growth and changes in crown structure for individual members of the stand can induce a series of secondary effects (Bennett and Hill, 1975; Murphy et al., 1977). Such changes proceed slowly and only the summation of annual effects gradually leads to higher morbidity. A slight change in the horizontal canopy structure will influence such habitat factors as incident radiation, precipitation, and pollution exposure to the lower-lying vegetation, causing extensive structural changes to the shrub and herb strata (Harward and Treshow, 1975).

In the aspen-fir forests of the Wasatch Mountains of Utah, aspen (Populus tremuloides) is the dominant and most sensitive species to photochemial oxidants (Treshow and Stewart, 1973). Shade from mature aspen is needed for optimal development of white fir (Abies concolor) seedlings. The increased light intensity from a thinning of the aspen stands as a result of photochemical oxidants endangers the natural reproduction of white fir. The opening of the stands also alters the precipitation relationships, displacing other species.

An eastern deciduous forest (Ohio River Valley, USA) experiencing intermediate dosages from a pollutant mixture showed a decline in species richness, evenness, and a decrease in the Shannon diversity index within all strata of the community (McClenahen, 1978). For example, the relative importance of sugar maple (Acer saccharum) declined in all strata, while the importance of yellow buckeye (Aesculus octandra) increased. Opposing trends in density were observed in some strata. Declines in the tree and herb strata were accompanied by increases in the subcanopy and shrub strata. These changes were attributed to more favorable light conditions in the lower strata and increases in shade-intolerant trees. Westman (1979) observed similar changes in the woody vegetation of the southern California coastal area and correlated them with changes in photochemical oxidant dosages. According to Harkov and Brennan (1979), the species most susceptible to ozone frequently belong to early successional stages and may therefore be especially endangered by ozone.

2.5.1.3 Low Pollution Dosage

The impacts of low dosages on vegetation lie on the borderline between the normal, i.e., unaffected, and significantly impacted vegetation. Depending on the concentration and exposure duration, effects can range from stimulations (see 4.1) to reductions in growth, reproductive capability, or susceptibility to abiotic and biotic stresses (see 3.3). Changes in competitive relationships may also occur, causing alterations in species composition (Treshow and Stewart, 1973). Under typical conditions, such effects can be detected only above a specific detection limit, i.e., response threshold. The detection limit has been lowered through the development of exposure systems using either filtered air with or without pollutant addition and field exposure systems (see 3.4). However, these systems can only be used on small to moderate-sized plants. Before detectable reductions appar in, e.g., growth, happen, various changes occur in biochemical, physiological, or substructural levels. The difficulties of establishing relationships between such processes and plant or community function are discussed in Section 3.1.2.

Vegetation may remove air pollution from the atmosphere without detectable effects on plant performance. The possible long-term effect on plants and plant communities is determined by the behavior of the specific substances in the ecosystem. Pollutants such as ozone and PAN which decompose rapidly cause effects through the summation of individual reactions over one or several years. With other components, e.g., heavy metals or N-containing components, they may enter into the nutrient cycles of the ecosystem causing cumulative effects (Krämer, 1976; Siccama and Smith, 1978) and distributing the balance of especially sensitive ecosystems.

In summary: under the influence of air pollution, two counter processes are initiated in plant communities. From direct and indirect effects, changes in the structure and function of the community occur. Parallel to this degradation, spontaneous or man-supported processes occurs in which either original, i.e., adaptively resistant members of the remaining community, and also immigrants undergo secondary succession (Guderian and Küppers, 1980b).

2.5.2 Causes for Observed Responses in Plant Communities

The effects of a given air pollutant on plant communities, as described in previous sections, ranged from insignificant changes to total destruction and are determined through:

-- genetically controlled resistance of individual community members;

-- moderating influence of environmental conditions on relative resistant relationships; and

-- pollutant-induced changes in inter- and intraspecific relationships.

The following presentation (Figure 4) attempts to clarify these relationships at the level of the individual, the homotypic population, considering intraspecific competition and the level of a heterotypic plant community.

The relationships among genetic, environmental, and resistance relations presented in Sections 4.2 and 4.3 for individual and also

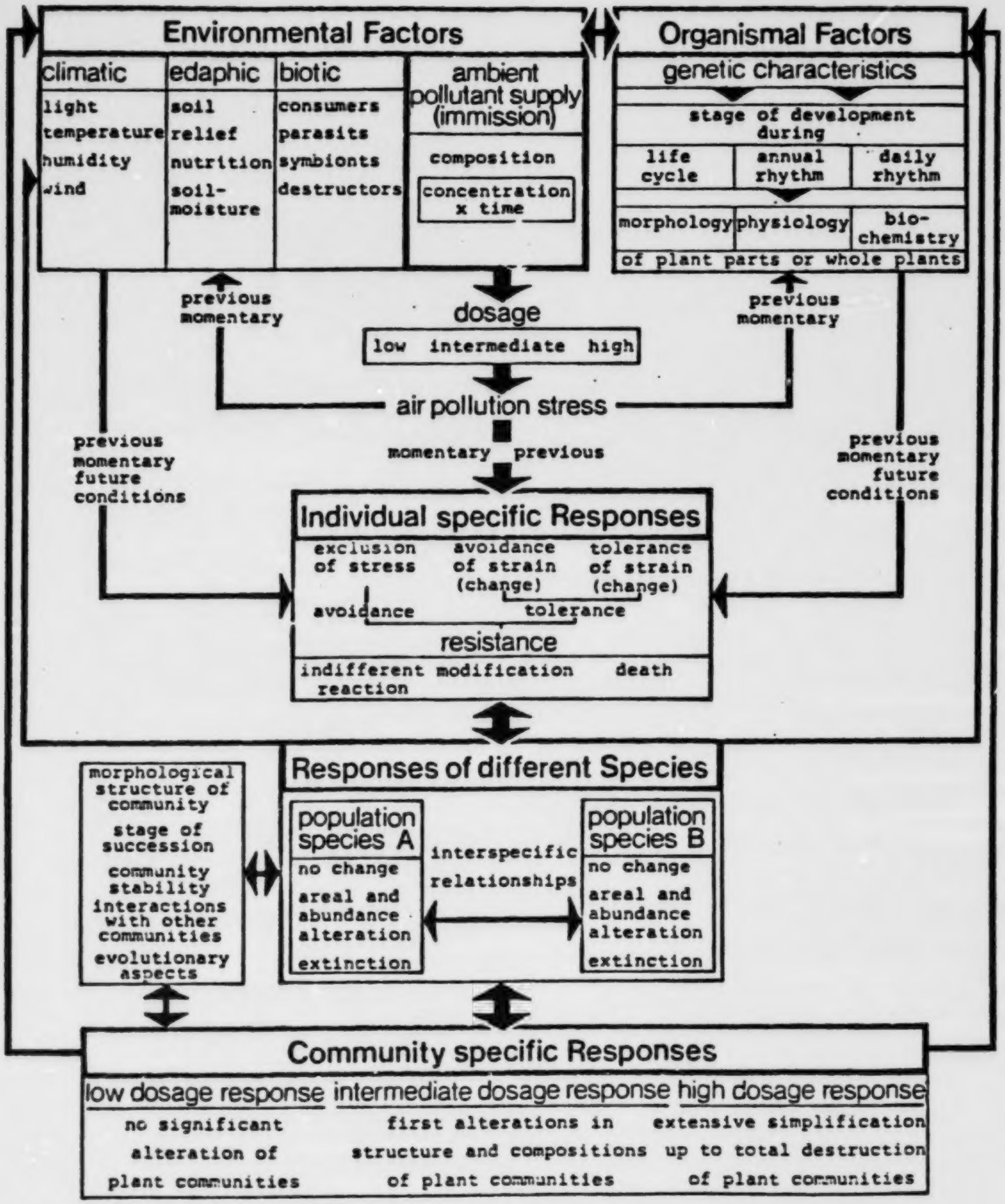
Environmental Factors
climatic
light
temperature
humidity
wind
edaphic
soil
relief
nutrition
soil-moisture
biotic
consumers
parasits
symbionts
destructors
ambient pollutant supply (immission)
composition
concentration x time
Organismal Factors
genetic characteristics
stage of development during
life cycle
annual rhythm
daily rhythm
morphology
physiology
bio-chemistry
of plant parts or whole plants
previous
momentary
dosage
low intermediate high
previous
momentary
air pollution stress
momentary
previous
previous
momentary
future
conditions
previous
momentary
future
conditions
Individual specific Responses
exclusion of stress
avoidance of strain (change)
tolerance of strain (change)
avoidance
tolerance
resistance
indifferent reaction
modification
death
Responses of different Species
morphological structure of community
stage of succession
community stability
interactions with other communities
evolutionary aspects
population species A
no change
areal and abundance alteration
extinction
interspecific relationships
population species B
no change
areal and abundance alteration
extinction
Community specific Responses
low dosage response
no significant alteration of plant communities
intermediate dosage response
first alterations in structure and compositions of plant communities
high dosage response
extensive simplification up to total destruction of plant communities

Figure 4. Effect-determining factors for various responses of plants at individual, species, and community levels (modified from Guderian and Küppers, 1980b).

homotypic populations also hold for plant communities; therefore, a discussion of them will be omitted. This presentation will focus on the community viewpoint.

The significance of the relationships shown in Figure 4 will be highlighted by the results from limited experiments on the relations between populations of different species. Studies on pure and mixed stands of ryegrass (Lolium multiflorum), hairy vetch (Vicia villosa), and crimson clover (Trifolium incarnatum) showed that pollution-dependent changes in the composition of the plant communities were not totally explained by the direct pollutant effects on the differentially susceptible species (Guderian, 1966); under the influence of SO_2, changes in the interspecies competitive conditions occurred. Thereby, the primary impact on the more susceptible members of the stand was so increased that they could no longer compete effectively for essential growth-determining factors such as mineral nutrients, water, light, and growing space; consequently, they lost their importance in the community structure. As a result of changed competitive conditions in the community, the decline of the more sensitive members permitted the enhanced growth of the more resistant species under low dosages. The total yield decreased less than would have been expected from the loss of the more susceptible species. Similar results were reported for ozone (Bennett and Runeckles, 1977), ultraviolet (UV-B) radiation (Fox and Caldwell, 1978), and ionizing radiation (McCormick, 1963).

The extent of changes in plant communities in response to a given pollutant burden depends on the condition of the community itself in addition to the previously mentioned genetic, environmental, and resistance factors. The importance of morphological structure, community strata, relief, and vegetative cover are discussed in Sections 2.5.1.1 to 2.5.1.3 as are the interrelations between successionary stages and system responses. The stability of a community influences the reactions of individual members as well as the whole community to a given pollutant exposure. Based on their complex feedback systems, highly productive ecosystems usually rapidly regain their equilibrium following minor disturbances. Under higher exposures, one must deal with obvious visual changes when individual key species are particularly sensitive to a given air pollutant, e.g., the dominant ponderosa pine in the San Bernardino Mountains (Taylor, 1973a, 1973b). But even low concentrations can cause considerable changes in semi-natural plant communities, especially when the aut- and synecological amplitudes of the indigenous community members are very divergent. Additional stresses from air pollutants, even at low doses, can induce drastic reductions in the vigor of plants already living outside their ecological optimum. The relatively high susceptibility of Norway spruce (Picea abies) in the Erzgebirge (Ore Mountains) of Czechoslovakia (Materna, 1972) and in the boreal coniferous forest in Finland (Huttunen, 1979) may result from their relatively unsuitable habitat. From this perspective, it seems problematic to transfer dose-response relationships derived from agricultural ecosystems in which plants encounter favorable growing conditions to natural ecosystems.

The relationships discussed here illustrate how pollution can degrade plant communities. However, it must be noted that spontaneous adaptation to air pollution stress has been observed adaptations which insure survival of the species not only through morphological changes such as "Kümmerwuchs," in which trees form a dense layered mat (Halbwachs and Kisser, 1967), but apparently through genetic changes also. Exposure of

Marchantia polymorpha to lead (Briggs, 1972) or various grass species to copper and zinc (Bradshaw, 1971, 1972, 1976) induced in a short time through directed selection the development of more tolerant populations. In a region experiencing variable SO_2 stress, tolerance to SO_2 developed in Geranium carolinianum over a 30-year period. Populations selected from around the source were more tolerant to SO_2 than those that had not evolved under the sulfur pollution (Taylor and Murdy, 1975). The consistent differences in SO_2 response among individuals was genetically controlled and quantitively inherited (Taylor, 1978b). Similar results have been reported for Lolium perenne and Rumex obtusifolius under chronic decade-long exposure (Bell and Clough, 1973; Bell and Mudd, 1976; Horsman and Wellburn, 1977).

Dunn (1959) found that subspecies of Lupinus bicolor from the Los Angeles Basin which had developed in the presence of photochemical oxidant air pollutant were more resistant to smog than their counterparts from nonpolluted locations. He hypothesized that the greater resistance to photochemical oxidant arose through the process of natural selection. The results of multi-year chronic SO_2 exposures to native grasslands (Preston and Gullett, 1978) also indicate that, under anything less than acute concentrations, spontaneous adaptations may occur in the course of forming a new secondary equilibrium which may also interrupt possible long-term injury (Preston, 1979). The evolution of plant resistance to air pollution has its costs, for example, in the reduced growth of resistant plants and altered adaptations in affected plant communities (Roose *et al*., 1982). Accordingly, the pollutant concentration and its frequency of occurrence should be controlled over the long term so that plant communities maintain the capacity for using the above-mentioned evolutionary processes to fulfill their function to the fullest in natural and agrarian ecosystems (Guderian and Küppers, 1980a). The genetic-controlled variation in populations as expressed in spontaneous adaptations also provides the basis for breeding population resistance through selection and propagation of relatively tolerant individuals (see 4.4).

2.5.3 Effects on Semi-Natural and Agro-Ecosystems

Pollution-induced transformations in plant communities and impacts on individual plants can lead to permanent impacts on economic, ecological, and environmental performance of vegetation. In agriculture and forestry, the damaging effects of reduced growth, impaired quality, and additional labor requirements are well documented. For individual sources of primary air pollutants, reliable pollution-induced performance reductions can, in general, be established. In contrast, for widely distributed pollutants such as photochemical oxidants, it is substantially more difficult to establish the economic loss. Only recently has man been concerned with the impacts on the ecological and environmental performance of vegetation in semi-natural ecosystems. Moreover, it needs to be established the ways in which air pollutants impact vegetation functions such as air filtering, climate stabilization, regulation of water and nutrient cycles, prevention of soil erosion, and the preservation of healthy habitats for zoo- and phytocoenoses.

In the agrarian ecosystem, the economic performance of the crop is the main interest. Photochemical oxidant-induced reductions in yield and quality can have direct economic consequences. In perennial crops such as fruits and forests, the reductions in growth, vigor, and/or reproduction can limit the biological basis of production. As a result of such documented impacts, researchers and agricultural constituents have attempted to assess the extent of pollution-induced injury as a basis for establishing possible mitigative actions. In addition, such data are useful from the economic and political perspectives for the decision-making process concerning alternative policies and the establishment of standards.

A reliable determination of photochemical oxidant-induced yield reductions in agrarian ecosystems is difficult to document. Even in agricultural systems devoted to annual crops, which are more easily cultivated and managed than perennials, the reports of photochemical oxidant-induced injury are divergent. Nevertheless, there are concrete proposals for obtaining reliable data. In forestry, the impacts of reduced height and radial growth on total wood production can be determined. But although there have been documented changes in secondary succession processes in some terrestrial ecosystems, the economic and ecological consequences of photochemical oxidant attacks on primary producers, consumers, and decomposers -- including host-pathogen relations -- are not obvious.

2.5.3.1 Damage Responses in Agriculture and Horticulture

The first report of photochemical oxidant air pollution impacts on agricultural and horticultural crops in the Los Angeles basin cited yield losses of $480,000 (Middleton et al., 1950). Since then, there have been repeated attempts to quantify the air pollution-induced agricultural losses. Two estimating methods have been used:

- Surveys of crops in the pollutant-impacted areas with assessments made for the locale and region.
- Use of dose-response relationships to make assessments for regional and multi-regional levels.

Both techniques provide only approximations. With local surveys, there are the inherent risks of false diagnosis; the damage intensity can not be determined precisely because the necessary controls for the widely dispersed pollutants are lacking. Also, the most common response measure, foliar injury, is not closely related to reduced growth and, in actuality, growth reductions may occur in the absence of visible symptoms or when the symptoms are not recognizable. No less serious are the potential sources of error for the second method: basically, dose-response relationships can only provide an approximation; assessment of pollutant exposures frequently are imprecise and their characterization may not indicate reliably the magnitude of risk to vegetation; the temporal and spatial extrapolation does not coincide exactly with actual exposure, and the climatic and edaphic factors deviate from the assumed conditions. Finally, the environmentally- and genetically-controlled resistances of the model plant do not correspond to the actual resistance of the impacted cultivars. The following discussion is presented within the parameters of these constraints in mind.

The field survey method has been extensively used in California to estimate the magnitude of yield reduction. For example, Middleton (1961) calculated the loss to agricultural plant species at 8 million dollars. Based on reports of 450 trained agricultural experts, the California Department of Agriculture estimated 1970 yield losses to agriculture at 26 million dollars (Millecan, 1971). Losses to citrus plants alone accounted for about 19 million dollars. Reductions not associated with visible injury were not considered except for grapes and citrus. Nor were monetary losses of native vegetation, including forests and landscape plantings, estimated. Approximately 50% of the damage resulted from ozone; PAN contributed an additional 20%. In 1977, the California Department of Food and Agriculture (1977) estimated pollution-induced crop losses at 31.6 million dollars for the five counties in the South Coast Air Basin (SCAB). In San Bernardino County, which received the highest ozone exposures, the mean yields of several crops were reduced about 20%.

The dose-response method has been used to estimate impacts at the regional and national levels in the USA. Based on the dose-response relationships from Larsen and Heck (1976) and using subjective conversion factors that related foliar injury to yield reductions (Millecan, 1971), Adams _et al_. (1982) estimated the primary losses to 12 vegetable crops, cotton, and sugar beets in four southern California regions at approximately 32 million dollars or about 5% of producers output. An additional $20 million in losses to consumers of these crops was calculated.

Estimated losses to crop production in the USA are shown in the following examples. Moskowitz _et al_. (1982) used the dose-response function of Oshima _et al_. (1976) and estimated yield losses for alfalfa as at least 4%. Adams and Crocker (1982) developed an _ex post_ estimate of the policy worth of the current National Ambient Air Quality Standards in terms of air pollution crop losses. The analysis focused on corn, soybean, and cotton, which account for about 60% of U.S. crop production. In each case, they used the species-specific dose-response relations from the National Crop Loss Assessment Network (NCLAN) and Heck _et al_. (1982) and four levels of ozone exposure to estimate the Marshallian economic surplus value (an economic measure approximating direct and indirect effects). The authors assumed that, without an ambient air quality standard, the ambient ozone concentration would increase to a level comparable to a standard of 0.18 ppm. A reduction from this level to the current USA ambient air quality standard of 0.12 ppm (1-hour averaging time not to be exceeded more than 1 day per year) produced an economic surplus for the selected crop species of about 3.4 billion dollars. Hence, the current standard was assumed to be yielding benefits of this magnitude for agriculture. The improvement of air quality associated with standards of either 0.10 or 0.08 ppm would produce an additional economic surplus value of approximately 1.1 billion dollars for each of the incremental improvements in air quality, yielding an additional surplus of 2.2 billion dollars with a standard of 0.08 ppm. The calculations assumed that these standards were achieved in the major agricultural regions of the United States.

Heck et al. (1982) estimated the annual USA crop loss at 1 to 2 billion dollars if the current National Ambient Air Quality Standard were obtained in all areas of the country; this corresponds to 2 to 4% of the total crop production. Ozone either alone or in combination with SO_2 or NO_2 accounted for 90% of the damage.

The National Crop Loss Assessment Network (NCLAN) was established to provide more accurate data on air pollution-induced losses to agriculture. "The NCLAN consists of a group of government and nongovernment organizations cooperating in field work, crop production modeling, and economic studies to assess the immediate and long-term economic consequences of the effects of air pollution on crop production. The program will define the relationships between yields of major agricultural crops and doses of O_3, SO_2, NO_2, and their mixtures. These relationships will be used to assess the primary economic consequences of the exposure of agricultural crops to these pollutants. The program is also designed to advance the understanding of cause-effect relationships with the intent of developing simulation models" (Heck et al., 1982). The NCLAN experimental procedures are intended to provide reliable data concerning the magnitude of crop production losses in the USA. A brief description of the NCLAN program and its initial results are presented. The data should be developed under conditions as nearly natural as possible to insure that the results are representative. Based on a detailed comparison of currently available methodologies, Heagle et al. (1979d) concluded that "open-top" field exposure chambers would produce the fewest artifacts. In the first year -- 1980 -- of the NCLAN program, experiments were conducted in "open-top" field exposure chambers at four locations in the USA having different climatic conditions: Ithaca, New York -- Northeast (NE); Raleigh, North Carolina -- Southeast (SE); Argonne, Illinois -- Central States (CS); Riverside, California -- Southwest (SW). Different species were exposed at each site:

NE -- red kidney bean (Phaseolus vulgaris L., cv. 'California Light Red')

SE -- peanut (Arachis hypogaea L., cv. 'NC-6') and turnip (Brassica rapa L., four cultivars)

CS -- soybean (Glycine max [L.] Merr., cv. 'Corsoy')

SW -- head lettuce (Lactuca sativa L., cv. 'Empire')

At each location, four replications six ozone exposures were used:

1. AA -- ambient air plot without a chamber;
2. CF (Control) -- charcoal-filtered air; this resulted in O_3 concentrations of 20 to 50% of ambient O_3 due to influx through the open top (in some parts of the country, this represents an approximate "clean" air background concentration);
3. NF-1 -- nonfiltered air with sufficient O_3 added for 7-h/day to compensate for system losses (about 0.015 ppm);
4. NF-2 -- as NF-1 plus an additional 0.03 ppm of O_3 for 7-h/day;

5. NF-3 -- as NF-1 plus an additional 0.06 ppm of O_3 for 7-h/day;

6. NF-4 -- as NF-1 plus an additional 0.09 ppm of O_3 for 7-h/day.

Initial results showed that the ambient air exposures (AA), when compared to the controls (CF), reduced the yields of the following crops: soybean 10%; peanut 14-17%; for one turnip cultivar 7%; head lettuce 53-56%; red kidney bean 2%. When a background ozone concentration of 0.025 ppm (seasonal 7-h/day mean) was considered, yield reductions were observed in all crops at seasonal 7-h/day (0900-1600 h standard time) mean ozone concentrations of 0.06 to 0.07 ppm when compared to the control concentrations. Results of subsequent research (Table 3) showed that, when yields between the control (CF) and ambient air (AA) exposures were compared, the yields of cotton and soybean were reduced by 14 and 5 to 19%, respectively. Yield losses were similar between the ambient air plots (AA) and the chambers (NF-1) which received a similar seasonal mean ozone concentration. Yields of 14 corn cultivars were not significantly reduced by the ambient air exposures.

Using results from (i) NCLAN, (ii) county-levels estimates of the seasonal 7-hr/day ambient ozone concentrations, and (iii) county-level statistics for crop distribution and crop production, estimates were made for the yield losses to the four major agricultural crops in the USA (Shriner et al., 1982). The county-level yield reductions were determined for peanut (sensitive), soybean (sensitive-intermediate), wheat (moderately sensitive), and corn (insensitive). These crops represent 62% of the acres harvested and account for 63.5% of the dollar value. Shriner et al. (1982) expressed summary data as yield increases expected if the ambient ozone concentrations were reduced to an assumed background of 0.025 ppm. Crop loss estimates developed by this assessment indicated that combined annual

Table 3. Reduced yields of soybean and cotton in relation to ozone concentration (results, 1981 NCLAN program).

	Crop/Location					
	Soybean/Northeast[a]		Soybean/Southeast[a]		Cotton/Southwest[b]	
Treatment	Ozone Conc. ppm	Reduced Bean Yield %	Ozone Conc. ppm	Reduced Bean Yield %	Ozone Conc. ppm	Reduced Bean Yield %
CF	0.017	0	0.025	0	0.021	0
AA	0.035	5	0.053	19	0.077	14
NF-1	0.035	8	0.055	19	0.071	20
NF-2	0.060	20	0.069	28	0.111	40
NF-3	0.084	31	0.086	40	0.143	41
NF-4	0.112	41	0.106	46	0.185	58

[a] Mean ozone concentration (7-hr/day) for 70 days.

[b] Mean ozone concentration (7-hr/day) for 111 days.

losses from ozone impacts may be as high as 3.1 (± 1.2) billion dollars for these four crops. Of that dollar loss, soybean accounted for approximately 64%, corn 17%, wheat 12%, and peanuts 7%. The major agricultural regions of the United States generally coincide with the regions experiencing elevated ozone concentrations. These economic crop losses represent only the primary impacts on producers; additional losses to consumers through higher prices and to agricultural processors would probably exceed those for producers. Beyond the crop impacts, the losses to forestry, ornamentals, landscape plantings, and the non-monetary losses to the ecological and environmental functions of vegetation have not been considered.

2.5.3.2 Effects on Semi-Natural and Forest Ecosystems

Agricultural and horticultural systems are composed primarily of annual plants, while in semi-natural ecosystems the vegetative cover contains a significant portion of perennial plants. Therefore, semi-natural ecosystems are particularly endangered from chronic oxidant exposures because small alterations accumulate over a period of years, producing greater long-term risk than those same changes in an annual agricultural crop.

2.5.3.2.1 Primary Producers

The long-term studies on photochemical oxidant impacts on vegetation in the San Bernardino Mountains have centered on ponderosa pine populations, a key species in the stands (Parmeter _et_ _al_., 1962; Taylor, 1973a, b, 1974a; Miller, 1973a; Kickert _et_ _al_., 1977; Miller and White, 1977). Parmeter _et_ _al_. (1962) found a decreased height growth in trees both with and without visual injury symptoms. Analysis of tree ring widths from period 1941 to 1971 showed that photochemical oxidants reduced the average annual ring about 2 mm compared to a previous corresponding period (Miller and White, 1977). Basal area, as a criterion, is better suited to measure effects on radial growth than annual ring width. Miller et al. (1977) estimated the reduction in total wood production by 30-year-old ponderosa pines in the San Bernardino National Forest (Figure 5). Total height, diameter at breast height, and wood volume for logs with 15-cm tops were determined. A simulation model of an eastern deciduous forest has been used to estimate changes in species composition and reduction in total biomass production for selected tree species (West et al., 1980).

Air pollutants can influence the reproductive capacity of plants through impacts on the number, size, nutritive content, and viability of seeds, as well as the mode of seed distribution, as has been shown in studies on SO_2 effects (Scheffer and Hedgecock, 1955; Pelz, 1963). Restrictions in the reproductive capacity of sensitive plants in the ecosystem is an additional competitive pressure.

The seeds from various pine and oak species provide a significant portion of the diet for numerous small mammals, such as western gray squirrel (Sciurus griseus anthonyi) in the San Bernardino Mountains. The squirrels store a major portion of the seeds they collect, contributing to their distribution. When seed production from Jeffrey and sugar pines (Pinus lambertiana) is decreased by photochemical oxidant, the squirrels consume a significant portion of the less desirable ponderosa pine seeds before they mature, decreasing natural reproduction (EPA, 1978b).

The briefly sketched results can be summarized as follows: if the present pollution exposures continue for several decades, then the pessimistic prognosis of Cobb and Stark (1970) will be verified: there

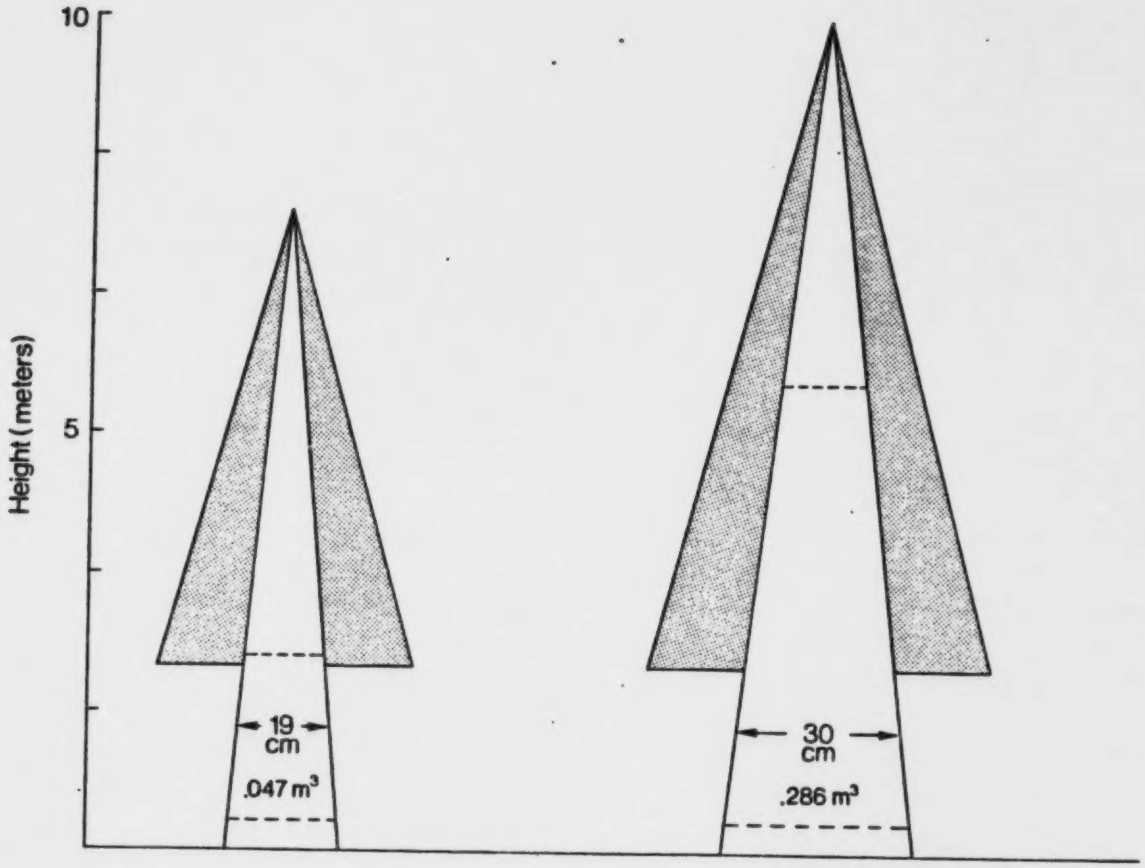
10
5
Height (meters)
19 cm
.047 m³
30 cm
.286 m³

Figure 5. Calculated average growth of 30-year-old ponderosa pines in polluted and nonpolluted air based on data from 1910 to 1940 and 1941 to 1971. Growth was determined as height, diameter at breast height, and total wood volume (Miller *et al.*, 1977).

will be a conversion from well stocked forest dominated by ponderosa pine to poorly stocked forests of less susceptible tree species in the San Bernardino Mountains.

2.5.3.2.2 Consumers

The effects of photochemical oxidants on consumers are both direct and indirect. The effects on indigenous animals and insects will be briefly described. If and to what extent photochemical oxidants directly influence the health, biomass production, and reproduction of indigenous animal populations cannot at the present time be assessed; however, certain direct effects on selection are nevertheless possible. Richkind and Hacker (1980) established that deer mice (Peromyscus californicus) from an area in Los Angeles experiencing high oxidant exposures were less sensitive to acute ozone exposures in laboratory studies than similar populations from areas receiving low exposures.

The reduced number of species in the San Bernardino Mountains in comparison to similar but unpolluted habitats (Miller _et_ _al_., 1977) rests completely or principally on the indirect effects or changes in food webs and habitats. The loss of specific plant species produces major impacts on species heavily dependent on it for food. From a habitat perspective, numerous animal species have only a limited ecological amplitude; consequently, alterations in the vegetation is an additional stress on the system that alters the variable relationships among animal species.

As observed in SO_2-impacted areas (Templin, 1962), the bark beetles (Dendroctonus brevicomis and D. ponderosae) increased on ponderosa pine in the oxidant-impacted forest stands in the San Bernardino Mountains (Stark _et_ _al_., 1968; Stark and Cobb, 1969; Taylor 1973a, b, 1974a; Dahlsten, 1978). The infection, i.e., mortality, in the forest stands clearly increased with photochemical oxidant exposure (Stark and Cobb, 1969). Long-term studies (1952 to 1972) in this area showed a significant increase in infections by these secondary pests, consequently increasing numbers of trees injured by bark beetles had to be logged (Miller et al., 1977). The higher tree mortality in forests over wide areas of the USA (U.S. Department of Agriculture, 1973) was caused by air pollution-induced increase in these infections by various weak parasites (Loucks and Williams, 1980). From theoretical grounds, Woodwell (1970) suggested that the increased occurrence of insects would cause a brief increase in specific vertebrate animals such as insectivorous birds.

The pollution-dependent alterations in the interrelationships in ecosystems can be very complex. For example, the gradual thinning of forest stands in areas heavily impacted by photochemical oxidants in the San Bernardino National Forest has caused a greater drying of soils; consequently, specific soil fungi will not form fruiting bodies. These fruiting bodies are significant food sources for squirrels and at some times of the year contribute more than a third of their diet. The squirrels' increased reliance on seeds from coniferous tree species will have a major impact on natural reproduction of stands (Miller and White, 1977).

2.5.3.2.3 Decomposers

It is not expected that photochemical oxidants will directly affect soil-dwelling decomposers. In fact, soils readily absorb ozone (Aldaz, 1969; Garland, 1976) where it reacts with the organic material or moist surfaces limiting its penetration (Blum and Tingey, 1977). In the San

Bernardino Mountains, microarthropod populations in moderately injured ponderosa pine stands were reduced 38% compared to uninjured stands (EPA, 1978b), but the cause was probably indirect. Initially, organic substrates were elevated by increased leaf and fruit drop (Miller et al., 1977); however, over the long term, photochemical oxidants reduced the biomass production of higher plants, providing less substrate for the decomposers. Under high oxidant impacts, there is a thinning of the plant canopy, promoting drying of the soils and soil erosion, which creates negative consequences for the decomposers. An increased loss of organic and inorganic materials through wind and water erosion from the ecosystem and decreased mineralization resulting from reduced and disturbed litter layers leads to a loss of mineral nutrients for primary producers, whereby biomass production is further decreased. In addition to the foregoing results that were primarily based on data from the San Bernardino Mountains, it is likely that additional effects will also occur, leading to the gradual destruction of photochemical oxidant-impacted ecosystems (Skelly et al., 1979).

2.5.3.3 Symbionts and Plant Pathogens

The symbiotic association between two organisms is based on a balanced exchange of metabolites. The equilibrium between the organisms is very labile and to a large extent susceptible to perturbations. Such perturbations can include air pollutants. This association also explains the high sensitivity of lichens, which are symbiotic organisms, to air pollutants (see Section 2.5.4). The symbiotic equilibrium can also be perturbed when only one of the symbiotic partners is affected by air pollution. An altered metabolite transport from the assimilatory organs to the roots influences the response of symbionts -- in the form of rhizobium-induced nodules on legumes or mycorrhizae on various plant species to photochemical oxidants. Ozone effects on the aboveground portion of legumes reduced the number, size, and weight of rhizobium nodules (Manning et al., 1971; Tingey and Blum, 1973; Blum and Tingey, 1977; Letchworth and Blum, 1977). The reduced nitrogen assimilation can have negative consequences for both the impacted plants and the ecosystem. Chronic ozone exposures of alfalfa reduced symbiotic nitrogen fixation (Tingey, 1977). Ambient levels of ozone in Ontario, Canada, were sufficient to reduce nitrogen fixation in red clover (Ensing and Hofstra, 1982). In addition, leaf leachates from fescue plants exposed to ozone have been shown to inhibit nodulation in white clover (Kochhar et al., 1980).

Disruptions of mycorrhizal symbiosis have been observed on both ponderosa and eastern white pine: the number of mycorrhizal roots were reduced and, in lieu of mycorrhizal fungi, saprophytic fungi increased, destroying the feeder roots (Parmeter et al., 1962; Miller, 1973a). Long-term ozone exposure reduced the infection of citrus seedling (Poncirus trifoliata x Citrus sinensis) roots by mycorrhizal fungi which resulted in reduced seedling growth (McCool et al., 1979). A short-term ozone exposure reduced spore production by the mycorrhizal fungus Glomus fasciculatus 50% (McCool et al., 1977).

As with symbionts, air pollutants impact the interrelations between the host plant and pathogen. Both qualitative and quantitive changes in host-pathogen relations can occur as influenced by the air pollutant, its dose, specific sensitivity of the host and parasite, and their developmental stages at the time of exposure. Air pollution is a widely dispersed allogenic factor which contributes significantly to the spread of multiple-pathogen diseases on plants (Heagle, 1973). It is difficult to establish the cause and extent of these complex diseases.

The system relationships between air pollution, pathogens, and their hosts can be analyzed from the following perspectives:

-- the direct effect of air pollution on the pathogen;

-- the indirect effect of air pollution on the pathogen;

-- the influence of the pathogen infection on the reaction of the host plant to air pollution.

Selected examples from this more specialized field of air pollution effects will be used to describe this problem in its basic themes, compilation, interpretation, and evaluation of detailed experimental results are contained in several summaries (Heagle, 1973; Saunder, 1973; Treshow, 1975; Manning, 1975; Treshow, 1980; Laurence, 1981).

Air pollution can both enhance and suppress infection, invasion, and activity of plant parasites; pathogens may also modify the sensitivity of host plants. Ozone displays bactericidal, bacteria static, and also fungicidal and fungi static activity. Therefore, under specific conditions, effects on the pathogenic organism are expected. Spores of the barley powdery mildew fungus produced fewer lesions when the plant received several subacute ozone exposures following inoculation (Heagle and Strickland, 1972). However, there were no differences in the spore germination rate, in contrast to Uromyces phaseoli, the cause of bean rust following relatively low sulfur dioxide doses (Weinstein _et_ _al_., 1975). Ozone had a major impact on the development of a functional host-parasite relationship in Erysiphe graminis f. sp. hordei by inhibiting the development of appressoria and penetration pegs (Schuette, 1971). Ozonation of Botrytis cinerea _in_ _vitro_ and _in_ _vivo_ decreased conidial germination, germ tube length, and pathogenicity (Krause and Weidensaul, 1978a). Exposure of Fomes annosus on an artificial medium to low ozone doses inhibited colony growth, the formation of air hyphae, and sporulation (Hibben and Stotzky, 1969). However, such results are not significant for practical environmental protection, as shown in numerous publications (Heagle, 1973; Treshow, 1980; Laurence, 1981), and as discussed in the following presentation. An example of numerous studies in which ozone induced no detectable effects on phytopathogenic organisms is the study of Heagle and Key (1973a) with wheat stem rust. Ozone exposures following inoculation during the penetration and infection phases, which were expected to be sensitive stages, had no influence on infection or the specialized infection structures. Stimulatory effects of ozone were found by Hibben and Stotzky (1969) during their studies on isolated spores of 14 fungal species at concentrations less than 0.25 ppm.

Air pollution can cause various alterations in the phyllo- and rhizosphere of host plants. Ozone injury to potato leaves provided an entry port for Botrytis cinera, increasing the infection compared to uninjured control plants (Manning _et_ _al_., 1969). Pollution-induced cellular leakage may also provide a growth substrate for pathogens (Pell _et_ _al_., 1977). On the other hand, extensive foliar injury can reduce the infection-susceptible leaf area (Laurence, 1981). In Geranium, ozone induced the formation of a "flocculent material" that by chemical or physical means hindered Botrytis cinerea infection (Krause and Weidensaul, 1978b). In the host plants, ozone can induce the formation of various compounds such as phenols (Section 2.4.3), isoflavonoids (Keen and Taylor, 1975), and increase peroxidase content that may be injurious to microorganisms. Laurence and Wood (1978) hypothesized that the inhibited infection of soybean by

Pseudomonas glycinea resulted from bacteria static effects of an isoflavonoid. It is not possible to determine if the lack of infection, in this case, resulted solely from the biocidal characteristic of the isoflavonoid. Tanaka (1976) hypothesized that the disease severity on poplars in polluted urban areas was the result of the simultaneous infection with Marssonia brunnea and ozone increasing the rate of plant-produced ethylene.

The significance of indirect effects on the interrelationship among air pollution, pathogens, and plants, according to our point of view, is the pollution-induced alterations in the predisposition of plants to biotic and abiotic factors. There are known secondary effects of air contaminants such as SO_2 (Wentzel, 1965; Grzywacz and Wazny, 1973; Huttunen, 1980) and, given the nature and extent of photochemical oxidant-induced change in higher plants, they support the conclusion of secondary effects from photochemical oxidants also, even though the data are limited. As described in Section 2.4, ozone and PAN induce various changes in metabolism that are frequently associated with reduced plant growth and vigor. Such weakened plants are especially susceptible to weak parasites such as bark beetles and facultative parasitic fungi. According to Manning (1975), the colonization of ozone-injured white pine needles was increased for the saprophytic Pullularia pullulans and reduced for the obligate parasite, Lophodermium pinastri. In contrast, Costonis (1968) found in inoculation experiments that both fungal species were more prevalent on ozone-injured needles than on control plants. In the Ruhr area which is polluted primarily with SO_2, Lophodermium pinastri is widely distributed on both pole and mature age stands of Scotch pines (Pinus silvestris); however, in clean air, this weak parasite occurs extensively only in young plantation stands with unfavorable water relations. Fomes annosus, a root parasite of conifers, is widely distributed in the temperate zones of both North America and Europe. In central Europe, this basidiomycete has attained a wide distribution in the last few years (Schütt, 1981b), and the increased incidence may follow the weakening of host plants by air pollutants such as SO_2 and photochemical oxidants, both singly and in combination. In this connection, the studies of Miller et al. (1977) are particularly important and differ from the laboratory studies of Hibben and Stotzky (1969). Ponderosa and Jeffrey pine seedlings exhibited a higher infection rate than unexposed control plants. Stump inoculations of differentially injured trees suggested that ozone injury increased the susceptibility of pine stumps to Fomes annosus (James et al., 1980).

Air pollution changes not only the predisposition to biotic, but also abiotic, stress factors. There occurs an interaction between SO_2 and winter stress in the boreal forests of Northern Europe, producing an injury response that was not observed previously (Huttunen, 1980). This response cannot be explained on the basis of dose-response relations determined under the less extreme cultural conditions of Central Europe. Additional risks to vegetation result from the co-occurrence of air pollution and water stress.

Numerous studies have determined the influences of pathogenic viruses on their host plant's reactions to ozone. A series of studies showed that virus infections reduced plant sensitivity to ozone for tobacco mosaic virus on tobacco (Bisessar and Temple, 1977) and tobacco ringspot on soybean (Vargo et al., 1978). The cause of the reduced sensitivity was attributed to reduced pollutant uptake through the stomata and also changes in plant metabolism (Laurence, 1981). In contrast to the above trends, tobacco streak virus infection increased the sensitivity of tobacco plants (Reinert and Gooding, 1978).

For practical environmental protection, three questions result from these briefly sketched themes:

- To what extent will the interactions among air pollutant, host plant, and pathogen alter the relationship between the air pollutant and the plant?
- Under what conditions should such changes be considered?
- How can such changes be recognized and quantified under practical conditions?

The last question relates to a diagnosis and the use of bioindicators, which are discussed in Sections 3.1 and 3.2. The first question is important for the assessment of the long-term risk to vegetation and is directly relevant for dose-response relationships used to establish standards. In agreement with Smith (1980), one should consider air pollution, above a specific concentration and for longer durations, as an allogenic factor which in natural and semi-natural ecosystems dominates the autogenic processes of succession. This includes changes in the mineral content of soils and plants and the sparingly studied host-pathogen relations and their importance to plant-community composition and their succession.

The conditions under which biotic and abiotic factors influence the relationships between air pollutants and plants depends on numerous factors, as is explained in Chapter 4. An example from these factors -- ambient concentration -- will be given from the research of Grzywacz and Wazny (1973) conducted in the vicinity of an SO_2 source. This study clearly showed that severity of infection depended on the pollutant concentration (Figure 6). As described by Scheffer and Hedgecock (1955), the conditions for the possible existence of fungi are lacking under high pollutant impacts. With decreasing exposure, the incidence of infection increased and then decreased to the level of the unexposed plants.

2.5.4 Community and Economic Consequences of Functional Disruption in an Ecosystem

The value of nature's free "goods" such as pure air, clean water, a harmonious climate, productive stands of vegetation containing numerous plant and animal species, has significance for man that can only partially be evaluated. Westman (1977) attempted to determine the pollution-induced reductions in the "non-monetary" performance of vegetation in areas such as climate regulation, stabilization of water relations, sorption of air pollutant, and reduction in soil erosion for the San Bernardino National Forest. He estimated a 27 million dollar annual cost for just the removal of sediment from water impoundments resulting from increased soil erosion from air pollution degraded plant stands.

A closed vegetation canopy increases the water storage capacity of the soil and reduces surface runoff, maximizing increases in groundwater. This benefits man not only through groundwater reserves, but with beneficial consequences for the climate. A healthy vegetative cover as part of an attractive landscape provides important opportunities for recreation.

At the present time, photochemical oxidants have been implicated as the cause of visible symptoms on various tree species in several national parks in the USA: Sequoia, Yosemite, Lassen, and Kings Canyon National Park (Williams et al., 1977; Williams, 1979).

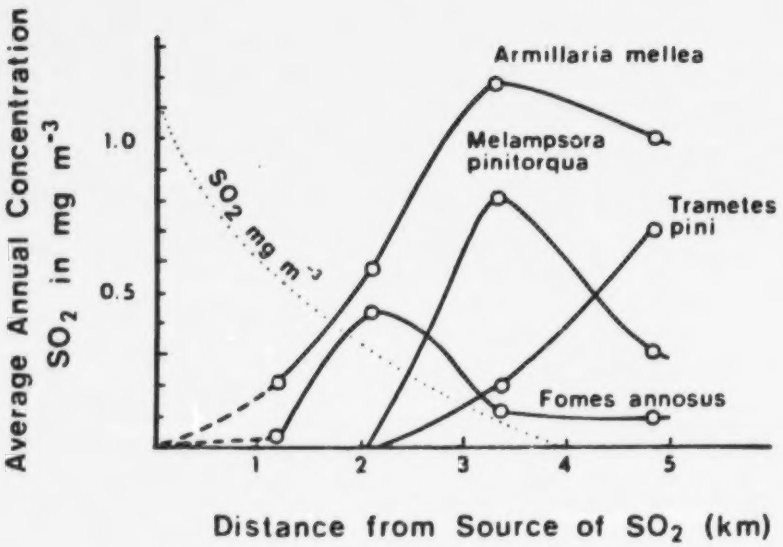

Figure 6. Average percent of trees infected with phytopathogenic fungi in relation to distance from an SO_2 source (Grzywacz and Wazny, 1973).

The preservation of species abundancy in nature is indispensible when evaluating man's present and future use, without even considering the ethical and aesthetic motives. The gene pool preserved in large species diversity provides a security that in the future biogenic and anthropogenic environmental changes can be responded to by flexible changes in the animal and plant world.

2.6 Effects on Lower Plants and Microorganisms

Few studies have investigated the effects of photochemical oxidants on lower plants and microorganisms. Higher plants have been the center of interest, primarily because of economic considerations. The fungicidal and bactericidal effects of ozone are well understood and, in practice, it is used as a disinfectant and preservative. Ozone effects on parasitic leaf fungi are also well documented. Single-celled green algae have been used to probe the biochemical and physiological modes of ozone action.

At the cellular level, it is assumed that the mode of action is similar for both higher and lower plants. There are differences in pollutant uptake as a result of morphological and anatomical differences in plant architecture. The thallophytes, in particular, display a high uptake rate when their thalli are in a hydrated condition. They lack cuticles and most other protective tissue. Based on the limited data, it is not possible to conclude that, in lower plants, these conditions result in a generally high sensitivity to photochemical oxidants. Nevertheless, it is surmised that, within an ecosystem context, the effects on lower plants are more extensive and intensive than previously noted.

2.6.1 Ferns

Photochemical oxidants effects on ferns have been observed only in the United States (Glater, 1956) and Japan (Kadota and Ohta, 1972) even though ferns generally are relatively sensitive. This sensitivity is a result of the anatomical and histological structure of the fern leaves which facilitates the distribution of absorbed pollutants throughout the spongy mesophyll tissue of the leaf. The absorption into the cells is expedited by the limited suberization of the cell walls. As a rule, the palisade mesophyll is not extensively developed. Therefore, the injury symptoms are substantially different than for higher plants. Glater (1956) described the characteristic symptoms on fern leaves following periods of elevated photochemical smog in the Los Angeles basin as "tan spotting of leaflets, followed by local or general dehydration of the affected areas, ending in necrosis of the entire leaf." The complete necrosis of numerous leaves was striking and leaf maturity had no influence on leaf sensitivity. However, the growing tip, roots, and vascular tissue were not affected unless the injury was extensive.

2.6.2 Mosses and Lichens

Mosses, based on their morphological, anatomical, and physiological organization as thallophytes, have a high capacity for pollutant uptake when they are hydrated. Several moss species can accumulate relatively high concentrations of heavy metals without injury, permitting their use as accumulator-bioindicators (Maschke, 1981); other species are very sensitive (Rao _et_ _al_., 1977). Acidic gases also cause substantial injury to mosses (Le Blanc and Rao, 1975a, b). Experimental studies on the effects of photochemical oxidants on mosses have received very little attention.

Comeau and Le Blanc (1971) found that a 4-h exposure to 0.25 to 1.0 ppm ozone stimulated the regenerative capacity of moss leaves, while a 6- to 8-h exposure was inhibitory.

A depletion in moss flora, particularly bark-dwelling (corticolous) mosses, has been observed repeatedly in the vicinity of large pollution sources and congested industrial areas. The extent of loss of sensitive moss species from photochemical oxidants is unknown.

The reduction of lichens in industrial and highly developed areas has received more study than mosses. It has been established, without a doubt, that lichens are good indicators of air pollution exposure. In numerous locations the distribution of epiphytic lichens has been used to establish zones of pollution exposure. Studies have shown that lichens are very sensitive to acidic gases (see, e.g., Ferry et al., 1973; Hawksworth and Rose, 1976).

Little is known of lichens sensitivity to photochemical oxidants or their modes of action. Sigal and Nash (1983) reported that the number of foliose and fruticose lichen species in southern California had decreased from 91 (Hasse, 1913) to 34. In the San Bernardino Mountains, which are ecologically well studied, the number of species decreased 50%. In a similar natural habitat, Cuyamaca Rancho State Park, which has experienced no significant pollutant exposure there was essentially no decrease from the original number of lichen species in (Sigal and Nash, 1983).

In the San Bernardino Mountains, the foliose lichen, Hypogymnia enteromorpha, occurred relatively frequently. However, compared to the Cuyamaca population the mean thallus size and fertility was reduced. At ozone doses of up to 150 ppm-h, the cover of Hypogymnia enteromorpha and Letharia vulpina in the San Bernardino Mountains was essentially normal

(Sigal and Nash, 1983). At increased doses up to 285 ppm*h there was a gradual decline in their cover until they were almost eliminated. Studies of epiphytic lichen species inhabiting black oak (Quercus kelloggii) revealed a 25% reduction in lichen species richness in the San Bernardino Mountains compared to similar habitats in the Cuyamaca area (Sigal and Nash, 1983). For other species, there was a significant negative correlation between ozone dose and lichen cover. In contrast, several resistant species were apparently unaffected by the photochemical oxidants.

Although the first observable ultrastructural changes occurred in the chloroplasts of the algal cells (Eversman, 1982), it was assumed that, as in higher plants, the primary site of effect on lichens was the membranes of the algal and fungal cells (Pearson and Henriksson, 1981). Because metabolite exchange between the symbionts occurs on membranes within the lichen thallus, membrane injury will disrupt the equilibrium between fungi and algae leading to a rapid disintegration (Jahns and Neumann, 1981).

There are no reports on the effects of photochemical oxidants on the exchange of metabolites between symbionts. However, effects on photosynthesis have been studied. Parmelia sulcata and Hypogymnia enteromorpha were exposed for 12 h with 0.5, or 0.8 ppm ozone. Both species demonstrated a significant reduction in gross photosynthesis at these ozone concentrations (Nash and Sigal, 1979). However, Parmelia sulcata was more sensitive, which may explain the observed reduction in the cover of this species in the San Bernardino Mountains (Nash and Sigal, 1980). Similar results were obtained following a one-week exposure with a low concentration of PAN (Sigal and Taylor, 1979). In Pseudoparmelia caperata, both short-term (0.1 to 0.5 ppm for 12 h) and long-term (0.10 ppm for 6 h/day for 5 days), ozone exposures reduced gross photosynthesis but the same exposures had no significant effect on Ramalina menziesii (Ross and Nash, 1983). Field observations in the Santa Monica Mountains in southern California, a region where ozone concentration may exceed 0.10 ppm between 50 and 100 days/year, suggested that P. caperata was undergoing stress (Ross and Nash, 1983).

The observation of Rosentreter and Ahmadjidan (1977) is confusing as they reported that a one-week exposure of the lichen or its algal component to 0.1 ppm ozone increased the chlorophyll content. Higher ozone concentrations had no effect. However, Brown (1980) suggested that this observation could be the result of inadequate experimental procedures.

Whether or not lichens can function as indicators to establish the cause of the presently occurring forest injury in Central Europe is unclear. On dead fir and spruce trees in the Bavarian and Black Forests of West Germany, Prinz et al. (1982) observed a more abundant lichen growth. Because epiphytic foliose and fruticose lichens are generally more sensitive to acidic gases than are coniferous trees, they concluded that the forest injury must be the result of other factors such as photochemical oxidants, or the lichens would not have outlived the trees. Brown and Smirnoff (1978) suggested that lichens were relatively tolerant of acute ozone exposures. They found that photosynthesis of Cladonia rangiformis was not affected by a 2-h exposure to 2.0 ppm ozone. In contrast, laboratory studies of three lichen species in Tennessee showed that they were more sensitive to ozone than acidic gases or acidic precipitation (Sigal, 1982). The sensitivity of lichen species, indigeneous to Central Europe, to photochemical oxidants is not known. Other factors, such as improved light relations as a result of the thinning of the crowns or the leaching of nutrients from injured needles, could contribute to the phenomenon of the lichens outliving the coniferous trees. This problem provides additional scope for studies of lichens and pollution ecology.

2.6.3 Algae

The relatively simple single-celled algae have been used to study the biochemical and physiological effects of photochemical oxidants on plants. These studies considered effects on membrane permeability, lipid budgets, and photosynthesis, and are discussed more fully in Chapter 2.4. In this section only a few significant aspects will be repeated.

To investigate changes in membrane permeability, extensive laboratory studies have used the ozone-enhanced loss of K^+ from Chlorella sorokiana (Chimiklis and Heath, 1972, 1975; Heath and Frederick, 1977, 1979). With short-term exposures the membrane injury was reversible but with higher concentrations or longer exposures it was not. There was an increased lipid oxidation, formation of malondialdehyde, and a decline in cell viability (Frederick, 1973; Frederick and Heath, 1975).

In addition to membrane injury and related disturbances, ozone reduced respiration (Heath, 1978) and photosynthesis (De Koning and Jegier, 1968a, b; Verkroost, 1974). Heath _et_ _al_. (1982) suggested that ozone effects on the photosynthetic processes were attributable to ionic imbalances brought about by ozone interacting with the plasmalemma rather than a direct effect on the chloroplast. In Chlamydomonas reinhardtii, PAN reduced photosynthesis, increased the loss of carotenoides and reduced chlorophyll _a_ and _b_ (Gross and Dugger, 1969). A one-hour exposure of Euglene gracilis to a combination of ozone and sulfur dioxide showed that they acted in an additive manner to reduced photosynthesis (De Koning and Jegier, 1970).

Results of these studies have provided data to help clarify the modes of action of photochemical oxidants on plants. Algal cultures were used because they can serve as an experimental model for higher plants and they are easily standardized (Heath et al., 1974). It is doubtful that the air pollutants, ozone and PAN, affect aquatic algae. It is not known if photochemical oxidants impact terrestrial algae growing on stones, soil, or tree bark.

2.6.4 Fungi

In natural conditions, fungi that live within the soil or in living or dead organic material are probably not affected by photochemical oxidants. The fungal fruiting bodies that project above the substrate, fungi dwelling on surfaces, and spores may be impacted (Watson, 1942). Studies concerning the effects of photochemical oxidants on fungi are mainly restricted to parasitic fungi because of their economic significance. The discussion in this section will be limited to the effects of photochemical oxidants, particularly ozone, on the fungi themselves and not the host-parasite relationship (see 2.5.3.3).

At relatively low concentrations, ozone is fungistatic or fungicidal and has been used in fruit storage (Harding, 1968). On an artificial cultural medium mycelial growth, the development of aerial hyphae, and spore production were restricted (Kormelink, 1967; Kuss, 1950). Rich and Tomlinson (1966, 1968) found that 0.1 ppm ozone for 4 h or 1.0 ppm for 2 h stopped the apical cell division of conidophores and resulted in the collapse of the apical cell walls of Alternaria solani, a foliar parasitic fungus. The apical and subapical cells swelled and elongation of the conidiphores was discontinued (Rich and Tomlinson, 1966). At a similar concentration range, ozone decreased the mycelial growth and spore production of the foliar parasitic fungus, Colletotrichum lindemuthianum (Treshow *et al*., 1969).

In several fungal species, ozone stimulated growth and spore formation. On agar culture media, increased spore production was observed in Alternaria oleracea (Kormelink, 1967; Richards, 1949; Treshow *et al*., 1969), Mycosphaerella citrullina (Richards, 1949), and Colletotrichum orbiculare (Hibben and Stotzky, 1969). Kuss (1950) found an increased spore production in 8 of 30 species grown on agar.

Spores generally appear to be relatively sensitive to ozone; their germination is easily restricted. Differences in the sensitivity of spores vary among species and are influenced by spore morphology, moisture, and the nature of the substrate (Hibben and Stotzky, 1969). Germination can be reduced over an ozone concentration of 0.1 to 1.0 ppm as shown by Hibben (1966) in laboratory exposures of ten parasitic fungal species grown on agar plates. In addition to reduced germination, the germ tube length and pathogenicity and/or virulence of Botrytis cinerea spores exposed to ozone (0.15 to 0.30 ppm for 6 h) *in vivo* and *in vitro* was reduced (Krause and Weidensaul, 1978a).

The types of culture medium can influence the ozone response. Fungal spores suspended in a liquid culture medium were less injured by ozone than spores on agar plates (Magdycz, 1972; Watson, 1942; Hibben and Stotzky, 1969). A portion of the ozone may have reacted with oxidizable substrates in the liquid culture medium, causing this difference. The type and hydration of the surface on which the spores are placed also influence the ozone response. Moist spores were substantially more sensitive to ozone than dry ones and spore germination was reduced to a greater extent on yeast extract-rose bengal agar than on water agar (Hibben and Stotzky, 1969). The substrate dependent differences in reduced germination observed in laboratory studies are expected to be more significant in natural conditions. In the field, the substrate (plant organ) on which the fungi are growing may be modified by photochemical oxidants, influencing the relationship between the parasitic fungi and its host. This association is discussed in Section 2.5.3.3.

2.6.5 Bacteria

Ambient air pollutant concentrations may also injure bacteria. De Mik (1973) subjected a microbial aerosol that was adhering to a gauze netting to various concentrations of air pollution. The rate at which the microorganisms died increased with the air pollution concentration. Corresponding studies with Escherichia coli showed that the death rate of this species was most correlated with the ozone concentration of the measured air pollutants in the ambient air (De Mik and De Groot, 1973). In other exposure studies (Pan et al., 1961), it was established that ambient photochemical oxidants reduced the growth of E. coli colonies. The magnitude of the reduction was primarily associated with the PAN concentration.

In humans, elevated ozone concentrations irritate eyes and mucous membranes. Similar concentrations are bacteriostatic. Goetz and Tsuneishi (1959) developed the "Biological Irritation Analog (BIA)" test in which bacteria were exposed to ambient air. The degree of growth reduction was analogous to the potential eye irritant from photochemical oxidants.

The bactericidal and fungicidal effects of ozone have extensive industrial applications. Germicidal ozone concentrations are used to disinfect drinking and waste water (Torricelli, 1959; Rice and Netzer, 1982; McCarthy and Smith, 1974; Burleson et al., 1975; Kinman, 1975; Schalekamp, 1982) and in the storage of fruits and vegetables (Smock and Watson, 1941; Schomer and McColloch, 1948; Nagy, 1959; Ridley and Sims, 1966). Even the storage life of eggs is increased with ozone (Krivopishin, 1974). Attempts to use germicidal ozone concentrations in climate controlled rooms have not realized full potential because of human health risks (Witheridge and Yaglou, 1939).

The toxicity of ozone to bacteria, as with fungal spores, is dependent to a large extent on the relative humidity and the moisture content of the substrate. When moist bacterial aerosols or suspensions were deposited on various surfaces, an ozone exposure (0.025 ppm for 0.5 h) at 70% relative humidity eliminated almost all of the bacteria but at a lower humidity the bactericidal activity was low, even at 1.0 ppm ozone (Elford and van den Ende, 1942).

As established in studies with animals, plants, microorganisms, and cell culture, ozone is a mutagen (Fetner, 1958, 1962; Davis, 1959; Feder and Sullivan, 1969; Zelac et al., 1971). Prior to mortality, mutations were induced in Escherichia coli with short-term exposures to 0.1 to 1.0 ppm ozone (Hamelin and Chung, 1974a, b, 1975) prior to mortality. The mutation frequency increased with ozone concentration and exposure duration. Some of the mutants were more sensitive to ozone, while others were more resistant than the "wild type strain." The ozone resistance was apparently associated with DNA repair mechanisms (Hamelin and Chung, 1976). The capacity for DNA-polymerase to repair ozone-induced defects in DNA appears to be important for survival, because there was found to be a correlation between the occurrence of DNA breaks and the mortality rate

(Hamelin et al., 1977). PAN reduced the transforming activity of isolated bacterial DNA, and in solution it reacted with the bases of the nucleic acids (Peak and Belser, 1969).

In conclusion, alterations in the permeability of the bacterial cell wall played an important role in injury and cell death (Scott and Lesher, 1963). Ozone altered the quantitative relationship between the phospholipids in the structure of the cell wall and interior membranes (Vokk, 1977).

Particular mention should be made of the reduction in the luminescence of photobacteria. This reaction was developed into a bioassay for air pollution (Serat et al., 1967). Reliable responses occurred when the ambient air contained 0.05 ppm ozone in short-term tests (Serat et al., 1969).

CHAPTER 3
DIAGNOSIS, SURVEILLANCE, AND ESTIMATION OF EFFECTS

In areas impacted by photochemical oxidants, it is particularly difficult to trace the pollutant-induced effects and risks to the source and determine the intensity and area affected. The occurrence of multiple air pollutants makes the identification of a specific phytotoxic component difficult and the visual injury symptoms are frequently of limited value. The extent of injury, i.e., reduced growth, quality, diversity, and the degree of risk, is difficult to assess over large areas, where air pollution-induced effects are frequently small in comparison to the variation in plant growth caused by climatic and edaphic factors.

Methods of diagnosis are presented in Section 3.1; the feasibilities and limits of plants as indicators are described in Section 3.2. The various plant reactions to ozone and PAN (Chapter 2) are differentially suited to estimate yield reductions of impacted plant species. The perspective from which response criteria are chosen and the ways in which these choices affect the corresponding evaluation of effects are the subject of Section 3.3.

3.1 Methods of Diagnosis

The positive diagnosis of air pollution impacts on plants with regard to its origin, expression, and area affected provides an essential basis for remedial measures. In environmental protection, pollutant-induced injuries play a role in establishing standards. Additionally they are frequently the basis for mitigative measures at sources and sites of impact and may serve as the basis for injury compensation in agricultural systems (Guderian and Vogels, 1982).

The general importance of diagnostic methods for photochemical oxidants is limited because it is not possible to establish a relationship between individual injury events and specific sources. In contrast to primary air pollutants, diagnosis of photochemical oxidant injury does not lead to reduction in emissions from individual sources nor compensation for yield reduction and impaired quality in the agro-economic system by an individual emitter. The remaining important tasks for diagnostic methods nevertheless require differential instrumentation for reliable identification as with any other air pollutant.

The diagnosis of pollutant-induced plant injury, when sufficiently characteristic visible symptoms are lacking, generally proceeds in two phases: (1) the exclusion of other possible abiotic or biotic causes, and (2) the recognition of the pollutant effect (Guderian and Van Haut, 1970; Malhotra and Blauel, 1980). Using various physiological and biological methodologies, it is possible to establish that the observed symptoms are not the result of other abiotic causes, such as unfavorable climate or soil relationships, or of biotic origin, such as animal injury, pathogenic viruses, fungi, or bacteria or a result of a disturbance in intra- or inter-specific associations.

Middleton _et_ _al_. (1950) were the first to establish the relationship between air pollution and injury on leafy vegetables, ornamental plants, and field crops that had been observed in the Los Angeles basin since 1944. Plant injury was thus the first indicator of the biological effects of photochemical smog (Haagen-Smit, 1952; Hull and Went, 1952; Thomas _et_ _al_., 1952; Middleton _et_ _al_., 1953; Stanford Research Institute, 1954). Richards _et_ _al_. (1958) identified ozone as a phytotoxic component during investigations of leaf injury in California vineyards. In the following years, ozone was recognized as the cause of injury to numerous agricultural and horticultural plant species and deciduous trees in many of the states in the USA (Heggestad and Middleton, 1959; Daines et al., 1960; O. C. Taylor et al., 1960; Hill et al., 1961). Also an injury of unexplained etiology, known as "ozone injury," or "chlorotic dwarf" on white pine in the east, or "chlorotic decline" on ponderosa pine in the western USA, was shown to result from exposure to photochemical oxidants, mainly ozone (Berry and Ripperton, 1963; Dochinger and Seliskar, 1970; Dochinger et al., 1970; Dochinger, 1968; Miller et al., 1963).

PAN-induced injury on spinach, beet (Beta vulgaris L.), lettuce, and mangel (Beta vulgaris var. cicla L.) was first established as an injurious component of photochemical smog by Middleton et al. (1950). The publications of Haagen-Smit et al. (1952), Bobrov (1952, 1955a), and Noble (1955) showed that the characteristic syndrome was injury to the lower leaf surface. Stephens et al. (1961) established that organic peroxides in photochemical smog were the cause of the injury, confirming a previous hypothesis of Haagen-Smit et al. (1952).

The direct diagnosis of air pollutant-induced plant injury follows the exclusion of other abiotic or biotic causes, and is supported by the results of the following investigations (Guderian and Vogels, 1982).

- Analysis of visible symptoms
- Analysis of subtle injuries
- Investigations of relative species resistance
- Plant analyses, chemical and physiological
- Soil analyses
- Air monitoring as well as simulation of the pollutant exposure
- Exposure of indicator plants

As a diagnostic method, the chemical analysis of plant and soil samples as indicators of pollutant accumulation is not useful as neither ozone nor PAN are bioaccumulated. The feasibility and limitations of indicator plants for diagnostic purposes are discussed in Section 3.2. Of the remaining approaches, phenomenological observations are doubtless of the greatest value since ozone and PAN-induced injury symptoms are reasonably characteristic.

3.1.1 Analysis of Visible Injury Symptoms

Morophological and anatomical changes in plants vary not only with the air pollutant but also with its concentration and duration of exposure. The symptoms are influenced by factors such as leaf age and developmental stage, which significantly impact the symptom distribution on the leaf and throughout the whole plant (compare 4.3.1).

3.1.1.1 Symptoms of Ozone Injury

Four types of ozone injury can be distinguished on leaves: pigmented lesions (stipple), bleaching, chlorosis, and bifacial necrosis (Hill *et al*., 1970). The first three injury types are generally characteristic reactions for chronic doses; bifacial necrosis results mainly from short-term acute exposures to high concentrations. Ozone preferentially attacks the palisade cells in the leaf mesophyll, a contributing factor to the ozone syndrome (Figure 7).

Pigmentation (stipple), the most common injury form on deciduous trees, shrubs, and herbaceous plants, occurs mainly on the upper leaf surface. The sharply defined small dot-like lesions or flecks result from the pigmentation or death of groups of palisade cells. According to the plant species, the lesion may be either dark brown, black, red, or purple; these colors result from the ozone-induced biosynthesis of specific

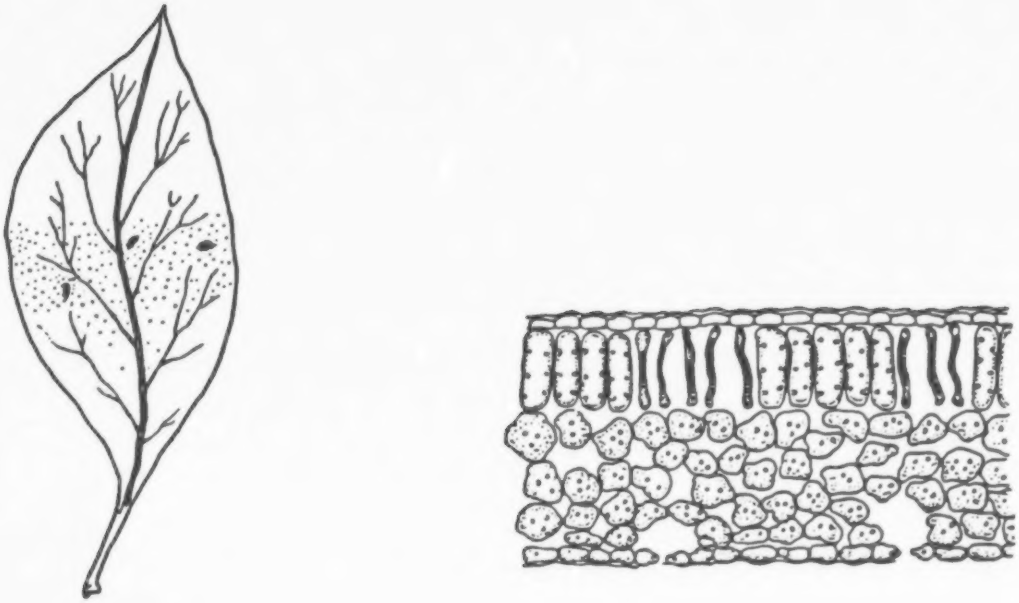

Figure 7. Ozone injury. Flecking (necrotic and chlorotic) and stipple effects on the leaf. On sectioning, the injury is localized primarily in the palisade tissue (Brandt, 1962).

anthocyanins and polyphenols (Koukol and Dugger, 1967; Howell, 1970, 1974). The pigments that accumulated in the injured areas of some plant species occasionally diffuse ito the adjacent tissue or veins. The primary injury occurs in the tissue bounded by the smallest veins so that angular or square lesions with rounded corners predominate. The epidermis above the injured palisade parenchyma remains, in general, uninjured. The symptoms are best observed at low magnification with transmitted light. The injury symptom described for grape leaves (Richards _et al._, 1958) is particularly characteristic.

As with stipple, bleaching occurs mainly on the upper leaf surface of many herbaceous and woody species. Numerous small necrotic, unpigmented lesions, or angular clearings of the leaf lamina impart a mottled appearance to the leaf. As the cells collapse, they usually remain connected to the healthy cells immediately above and below, and the resulting air-filled spaces impart a light gray, milky white, or tan-colored appearance to the leaf. On numerous dicotylendonous plant species, e.g., tobacco, pinto bean, soybean, and plane tree, the symptom occurs in "classic" form. On species such as small grains and grasses that lack a differentiated mesophyll tissue, injury may occur on either leaf surface.

Chlorosis, as with the previously described symptoms, occurs almost exclusively on the upper surface of leaves with palisade parenchyma. The primary lesions are usually limited to small groups of palisade cells. The overlying epidermal cells and the underlaying spongy mesophyll cells usually remain uninjured. The lesion size ranges from only a few cells to flecks approximately 1 mm in diameter. With chronic or repeated exposures, the injured areas may coalesce, giving the leaf a mottled appearance. Microscopic examination showed that most of the chlorotic cells were still alive, but the chloroplasts were disrupted and the chlorophyll content was reduced (Hill _et al_., 1961). Chlorotic mottling or chlorotic flecks are common symptoms on pines, but on other plant species they occur less frequently than stipple or bleaching. On grasses or plants with an undifferentiated mesophyll, a fine chlorotic fleck usually develops between the veins on both leaf surfaces. The outer spongy mesophyll cells adjacent to the vascular bundle sheath and cells overlying small vascular strands appear to be most readily affected but chlorosis may extend through the leaf (Hill _et al_., 1961). Under long-term, persistent exposures or several days after higher concentrations the leaves will prematurely senesce and abscise (Ledbetter _et al_., 1959).

Bifacial necrosis occurs when the mesophyll tissue between upper and lower epidermis is destroyed. The upper and lower epidermis are drawn close together to create a thin papery lesion that, depending on the species, ranges in color from white to red-orange. Small veins are usually injured, while the large veins survive unless higher ozone concentrations occur. Bifacial necrosis and other injury symptoms, appearing only on the upper leaf surface, frequently occur on the same leaf.

The course of injury development from high concentration, short-term acute exposures can provide diagnostic information. The first symptom of injury is a swelling of the palisade cells and raising of the epidermal cells. The injured leaf portions appear water-soaked or oily as a consequence of increased membrane permeability and the movement of water into the intracellular spaces (Smith, 1970). At this stage, injury development is reversible; if the pollutant concentration decreases or a pollutant-free period occurs the symptoms will disappear. With continuing exposures, the palisade and spongy mesophyll cells shrink and desiccate, producing bleaching and bifacial necrosis.

The value of visible symptoms as diagnostic evidence is significantly increased when the injury distribution on the leaves and the whole plant are considered. The influence of leaf age and development stage on the type, range, and distribution of visible symptoms is considered further in Section 4.3.1.

The previously described ozone symptoms do not adequately depict the types that occur on conifers. Three classic syndromes of ozone injury on conifers are: "ozone injury" and "chlorotic dwarf" of eastern white pine and "chlorotic decline" of ponderosa pine.

The name "ozone injury" originated with Sinclair and Costonis (1967), and Costonis (1968) for the ozone-induced injury that was previously identified as "emergence tipburn," "white pine blight," or "white pine needle die-back" of eastern white pine (Berry and Ripperton, 1963). Histologically, injury to conifer needles begins with the collapse of the palisade cells adjacent to the stomatal pores, forming silver flecks which radiate from the stomata. Initially, the endodermis and stele are unaffected, but when shrinkage and chlorosis occur they are disrupted (Costonis and Sinclair, 1969a, 1969b). The syndrome of this widespread disease in the eastern USA is expressed through tip die-back on the young -- one-to-six weeks old -- developing needles. The partially mature tissue is the most severely injured; nevertheless, immature and fully developed tissue are also affected. The disease should not be confused with "semi-mature-needle blight" (SNB) which is not ozone caused (Linzon, 1967). In general, the ozone injury develops from chlorotic flecks into pink lesions and bands followed by a spreading orange-red necrosis which may take one to two weeks to reach the needle tip on sensitive trees while the resistant trees may display only chlorotic flecking or mottling. The injury reduces needle retention from approximately three years on healthy trees to approximately one year; on sensitive trees the needles senesce prematurely leaving only current year needles by mid-summer with consequences for shoot, radial, and root growth.

"Chlorotic dwarf" of eastern white pines, which has been identified for more than 70 years (Spaulding, 1909), reflects a physio-genetic condition characterized by stunted root and shoot growth, mottled needles, and premature needle drop (Dochinger and Seliskar, 1965; Dochinger, 1968; Dochinger *et al*., 1970). The needles on genetically susceptible trees start to develop normally, but chlorotic flecks soon develop. The older needles turn prematurely yellow and are shed before the young needles have fully developed. In the final stages of the disease, particularly following a drought, the current year needles develop a tip-burn. The disease occurs most commonly on young trees in plantations. Severely injured trees tend to succumb within the first 15 years. In a population, individual trees exhibit considerable differences in susceptibility. While the less susceptible individuals display only mild mottling and nearly normal needle length, the more susceptible individuals display yellow mottling, possibly curled needles and stunting of all plant parts. Following etiological studies, Dochinger *et al*. (1965, 1970) demonstrated that "chlorotic dwarf" was caused by air pollutants, including ozone or a combination of ozone and sulfur dioxide.

"Chlorotic decline," "X-disease," and "ozone needle mottle" are three synonyms for an important air pollutant-induced disease on ponderosa pine in California. The name "X-disease" stems from 1953 (Asher, 1956) when an injury of unknown etiology was first observed, while the terms "ozone needle mottle" (Richards et al., 1968) and "chlorotic decline" (Parmeter et al., 1962) were coined later. Ozone transported into the forests from urban areas on the Pacific Coast was identified as the causative agent (Miller et al., 1963; Miller et al., 1969). Chronic ozone exposure induces chlorotic mottle symptoms which develop from needle tip to base, eventually followed by necrotic tip die-back. The older needles senesce prematurely with the chlorotic areas coalescing and turning a uniform tan color. Because of the premature needle drop, severely affected trees retain only one-year-old needles while on uninjured trees three- to five-year old needles occur. Extreme variation in susceptibility to chlorotic decline is found in the forests with dead and dying trees growing alongside visibily unaffected ones.

Ozone injury occurs less frequently on fruits and blossoms than on assimilatory organs. Ozone injury on apples appeared as either a raising of the lenticels or a collapse of the tissue around them (Miller and Rich, 1968). The necrotic flecks were gray to dark brown, 1 to 2 mm in diameter, and separated from the healthy tissue by a corky layer approximately 1 mm thick. On bean pods, rows of necrotic lesions developed during growth (Weaver and Jackson, 1968).

Flower formation was reduced by long-term chronic ozone exposures of petunia, geranium, and carnation (Feder and Campbell, 1968; Feder et al., 1969a; Feder, 1970a). Flower formation was particularly impacted if the exposure occurred during flower induction (Feder and Campbell, 1968). Ozone-induced yield reductions for citrus and grape crops in California are thought to result, in part, from reduced blossom formation (Thompson, 1970; Thompson and Kats, 1970).

Pollen is particularly sensitive to ozone. Tobacco pollen germination and pollen-tube elongation were reduced 40-50 and 50%, respectively, following exposure to 0.1 ppm ozone for 5.5 h (Feder, 1968). Similar results were obtained from exposure of corn pollen (Mumford et al., 1972).

In addition to the described symptoms, photochemical oxidants can cause premature fruit drop (Weaver and Jackson, 1968; Thompson et al., 1970), which has caused reduced yields in citrus groves in California, USA (Richards and Taylor, 1961; Thompson, 1968), and field beans in Ontario, Canada (Weaver and Jackson, 1968).

3.1.1.2 Symptoms of PAN Injury

The first symptoms of what is now called "PAN injury" were described by Middleton et al. (1950) in their report, "Injury to herbaceous plants by smog or air pollution." The higher homologs of PAN (peroxyacetyl nitrate) such as peroxypropionyl nitrate (PPN), peroxybytyryl nitrate (PBN), and peroxyisobutyryl nitrate ($P_{iso}BN$) produce symptoms indistinguishable from PAN. Characteristics of the syndrome include glazing, silvering, and bronzing of the lower leaf surface of dicotyledonous plants such as spinach, beet, Swiss chard (Beta vulgaris cicla), or mangel (Beta vulgaris flavescens) (Middleton et al., 1958; Taylor, 1969). It is possible that the foliar injury symptoms on tomato (Pearson et al., 1974) and petunia (Lewis and Brennan, 1978) in the northeastern United States attributed to PAN may also be induced by exposure to the combinations of ozone and sulfur dioxide (5.2.3). Under some conditions PAN and ozone may produce similar symptoms on petunia and annual bluegrass (Tonneijck, 1983a). Microscopic analyses indicate that protoplasts of the spongy mesophyll are collapsed, especially in the region of the stomata. The resultant air spaces contrib-

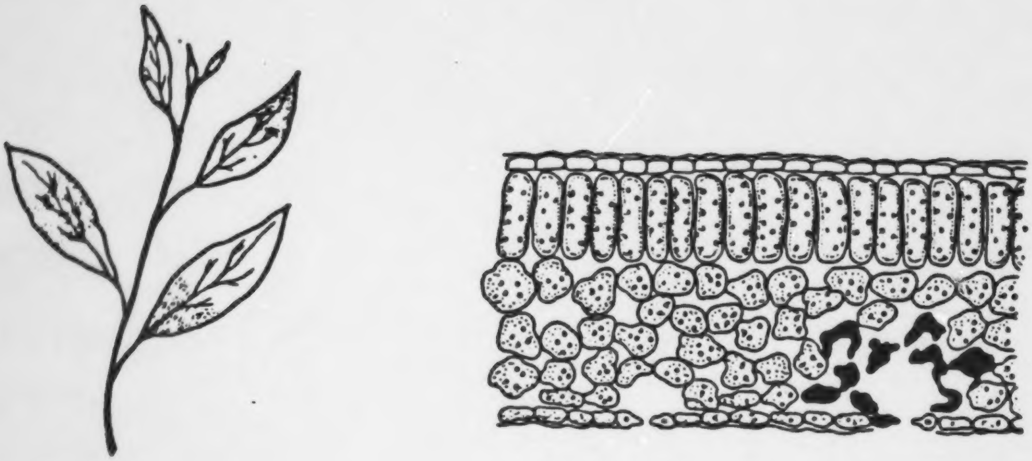

Figure 8. PAN injury. Leaf age influences the location of injury; the susceptible tissue progress from leaf tip to base as the leaf matures. On sectioning, the injury is located primarily in the spongy parenchyma tissue (Brandt, 1962).

ute to the typical injury pattern (Figure 8). The epidermis is not directly injured. When the PAN concentration is increased, the palisade mesophyll cells are affected producing brown necrotic spots with glassy margins. Bifacial necrosis occurs more frequently in monocotylendonous than in dicotyledonous plants (Bobrov, 1955a, b) and on plants with undifferentiated mesophyll tissue. Also, PAN causes distinct transverse bands across the monocot leaf from a few mm to perhaps 2 cm wide with the bands occurring in the same location on leaves of the same age. On several grass species, the injury occurs as longitudinal streaks that are associated with the stomatal distribution. Symptoms of chronic PAN injury have not been previously described; only the symptoms occurring in the field under the impact of the photochemical smog complex.

The PAN symptoms on ferns deviate from those observed on mono- and dicotyledonous species. Ferns have an undifferentiate mesophyll tissue with large intercellular spaces, permitting the rapid distribution of PAN throughout the leaf. Injury initially appears as bright yellow necrotic spots, progressing to complete leaf necrosis with continuing exposure (Glater, 1956). Differential sensitivity of various portions of the leaf was not observed with ferns.

A diagnostic clue, in addition to the described symptoms, is the development of the injury. The first visible sign of injury is the development of a slightly oily or waxy appearance to leaves followed by glazing. The final symptom, i.e., bronzing, is an advanced stage and occurs 2 or 3 days after exposure.

3.1.2 Subtle Injury

When classifying pollutant effects on plants, the distinction is frequently made between "visible" symptoms, i.e., necrosis, chlorosis, or pigmentation, and "invisible" symptoms which cannot be established by external changes. This terminology, introduced by Sorauer and Ramann (1899) has been extensively debated, and with time enlarged upon and modified (Haselhof and Lindau, 1903; Stoklasa, 1923; Reckendorfer, 1952; Kisser, 1966) and discussed under various names, e.g., "hidden," "latent," "physiological," or "subtle" injury, but it is still basically pollutant-induced reductions in plant performance or vigor without visible, external symptoms.

Numerous attempts have been made, without success, to verify this logically based postulate; in this respect "invisible" injury, for example a reduction in growth, should be viewed as a result of alterations in plant metabolism, or cellular ultrastructure. During the last three decades, there has been a substantial improvement in the available methods to determine the occurrence of such injury. Since the early reports of "invisible" injury (Hull and Went, 1952; Koritz and Went, 1953) by photochemical smog, additional observations have been made. Chronic ozone exposures reduced alfalfa growth without visible injury (Tingey and Reinert, 1975) and the height and specific gravity of poplar stems (Patton, 1981). Also, growth reductions have been observed in the absence of visible injury for other pollutants: ethylene (Abeles and Heggestad, 1973; Heck and Pires, 1962), PAN (Temple, 1982), sulfur dioxide (Tingey and Reinert, 1975; Guderian, 1977), and HCl (Guderian, 1977).

The increasing importance of subtle changes in plants for practical environmental protection measures results from the reduced performance of plants as economic objects in agriculture and forestry at the present chronic exposures to low concentrations. Beyond that, newer results have increasingly shown how subtle effects can change the predisposition of plants to biotic (Laurence, 1981) and abiotic (Huttunen, 1980) stress factors. Naturally, the criteria for the early indication and detection of such effects has achieved a central importance.

The difficult-to-recognize effects include not only reductions in growth and changes in predisposition in the absence of external, visible symptoms, but also reduced performance when only chlorosis, pigmentation, or premature senescence occurs. This is especially true for photochemical oxidants that cover large areas. With frequent chronic exposures, not only can visible injury symptoms be lacking, but also given relatively homogeneous concentrations over large areas, the clearly defined injury gradients associated with sources emitting primary air pollutants are not present. At the same time, photochemical oxidants pose a particular risk to vegetation from latent reductions in performance: for example, in areas receiving typical photochemical smog exposures, there is frequently an insufficient period between exposures for plant recovery; also chronic exposures are influenced by a wider range of ecological conditions than acute exposures.

For these reasons, it is necessary to develop and use methods for early detection (Keller, 1981). For this purpose, biochemical and physiological criteria from the cell or organelle levels of organization will be used to show their suitability as indicators (Guderian and Reidl, 1982). Changes in enzyme activities, alterations in pigment contents, increased ethylene production in plant tissue (Tingey, 1977), reduced ATP biosynthesis (Flueckiger _et_ _al_.,1978), reduced photosynthetic rate or disturbances in plant water relations can be applied as early indicators of air pollution stress. The ozone-induced enrichment of zinc, copper, and cadmium in grain may also provide an early indicator (Blessin et al., 1979). An example of a sensitive indicator of air pollution stress is peroxidase activity. Numerous plant species under the influence of various air pollutants displayed an increased peroxidase activity as an indicator of premature senescence (Keller, 1974; Rabe and Kreeb, 1979). In such studies it is possible, generally before the appearance of visible injury symptoms, to detect air pollution-induced stress. This is particularly important for perennial plants in which small changes in plant metabolism can, during the course of time, cause significant reductions in performance (Huttunen, 1980). The value of biochemical, physiological, and ultrastructural changes in cell organelles is limited because the changes are generally not specific and are frequently reversible, reflecting only the current conditions. Also, it is difficult to relate biochemical and physiological alterations to effects noted in individual plants, populations, or communities.

3.1.3 Investigations of Species Specific Resistance Relationships

Individual plant species, cultivars, plant provenances, individuals and their respective populations react with differential sensitivity to various air pollutants (see Section 4.3.2). This differential sensitivity can be of diagnostic value when the degree of injury on plant species in the study area is compared to established relative plant resistance listings for the suspected air contaminant. Therefore, it is important to examine the criteria used to establish the relative resistance which are different than the criteria used for detection and evaluation of an effect.

Most relative resistant groupings for individual species have been based on visible foliar injury (Jacobson and Hill, 1970; Davis and Wilhour, 1976) rather than plant yield. The pollutant-induced changes in the vigor and survival of individual differentially susceptible plant species through, in part, altered interspecific competitive conditions should be considered when identifying impacts on plant communities (Guderian, 1977; Wolak, 1977). Alterations in plant communities, according to our present knowledge concerning their responses to photochemical oxidants, are less suited for etiology than for determining the intensity and spatial distribution of pollutant impacts. The uses of synecological changes as a method of bioindication will be discussed later.

3.1.4 Air Monitoring

The procedures presently available permit the reliable determination of the atmospheric content of ozone (see 1._._.) and PAN (see 1._._._.). The ascertainment of a correlation between the ambient concentration and plant effects is an additional prerequisite for using monitoring equipment in the diagnosis and evaluation of oxidant impacts. However, it should be remembered that air monitoring only provides information concerning the probable risk, not the nature of effect. Whether an effect occurs depends not only on the concentration and duration of exposure to a particular air pollutant, but also on the relative sensitivity of the exposed plant species as influenced by the climatic and edaphic conditions. Air monitoring methods only describe the instantaneous ambient concentrations; they do not provide reliable information concerning the pollutant exposure at the time of injury. This is especially true for secondary pollutants that are formed in the atmosphere and display large time dependent concentration changes, frequently to a greater extent than primary air pollutants. Also, a high level of technical expertise is required to measure ozone and PAN in the ambient air which diminishes their value in diagnosis. Nevertheless, measurements of ambient concentrations have their value, because they can provide information on the probability that an effect may result. With primary pollutants it is possible to simulate the probability of pollutant exposure using emission data and diffusion modeling but this has been less successful for secondary air pollutants.

3.2 Bioindicator Plants

For photochemical air pollutants, the development of preventative measures for environmental protection in either the prophylactic or retrospective sense is very difficult. Photochemical oxidants occur over large areas and form complex mixtures, composed of numerous ecotoxicological components which interact with each other and primary air pollutants, posing a particular risk to vegetation. Improved chemical and physical methods of air monitoring make it possible to identify and measure the most important phytotoxic components; however, because of technical limitations and expense, it is not possible to measure all potentially phytotixc components or to accurately assess the potential risk of such a pollutant complex. Above all, measurements of ambient concentrations can be used only for risk prognosis, not to predict actual responses. The extent to which a specific episode may be injurious depends not only on the pollutant exposure, but also on the genetic and environmental resistances of the exposed plants. Consequently, chemical and physical air monitoring as the only methods are insufficient to determine the degree and origin of pollution-dependent risks. A reliable expression of the actual vegetation response is only possible by determining the effect. Organisms are particularly well suited for the detection, determination, and evaluation of air pollutants because they can demonstrate the effect of the pollutant. For this very reason, the use of organisms is increasing in environmental protection.

Plants, in addition to other organisms, respond to external stimuli such as air pollutants in numerous ways. Their responses to this stimulation provide criteria suitable for indicator purposes. The differences in the activity of air pollutants are expressed in various quantitative plant reactions. Plants can serve as indicators of the biological activity of air pollutants because they are not only sensitive, but frequently provide specific responses to the prevalent air pollutants. Moreover, comparative studies are easier with plants than with animals or humans, because plants are usually found in large numbers in specific habitats and are exposed to environmental conditions that are easily determined.

A bioindicator must meet various requirements as expressed in various definitions of this concept. For example, Ellenberg (cited in Kohler, 1978) defined a bioindicator as, "a group or community of organisms whose presence or other easily measured behavior is so closely correlated with the specific attribute that one can use it as an indicator or a quantitative test." This broadly based definition would also include indicator plants which reflect the characteristics of a site, for example the soil or climate. However, in this section, bioindicators will be considered as only those organisms whose reactions reflect the anthropogenically-influenced environmental factors.

3.2.1 Bioindicator Methods

To establish pollution-induced effects, one can choose between effects on cultivated and native plants grown in their natural habitats, "passive monitoring," or from standardized methods of plant culture and exposure in the areas under evaluation, "active monitoring." In the first case, except for the use of the recently available exposure systems with and without air filtration, all parameters, beginning with the indicator and including the various internal and external growth factors that influence the response, must be accepted, while in the second case, they are partially regulated. The laboratory-based "Biotest" will not be considered because it is not well suited for use with photochemical oxidants.

All three procedures can be used at various biological organization levels such as plant community, population, organism, organ, and organelle. "Passive monitoring" includes all reactions that have an "indicator" function, i.e., changes in the community composition or phenomenalistically confirmed injury symptoms on populations or individuals provide a preliminary indication of impacts on an ecosystem. "Active monitoring," particularly the "Biotest" with its controlled and reproducible conditions, provides a better basis, aided by physiological, biochemical, and electronic-optical methods, to determine alterations at the cellular or subcellular levels. Different expressions and application possibilities arise from these procedures: "passive monitoring" is well suited for diagnosis (3.1), while "active monitoring" is better suited for detecting the gradation of impacts related to surveillance.

3.2.1.1 Passive Monitoring

3.2.1.1.1 Autecological Procedures

For the recognition of air pollution-induced injury, the identification of its cause, and the determination of the injury intensity on cultivated and native plants in their natural habitats, the autoecological factors are more important than the synecological ones. Since the beginning of systematic studies of air pollution injury on vegetation, about 130 years ago, injury responses have repeatedly provided the first indication of pollutant impacts. The results of studies on individual plants or populations of individual species have aided in the identification of, e.g., sulfur dioxide (Stöckhardt, 1871), thallium (MAGS and MELF, 1980), and photochemical smog (Middleton _et_ _al_., 1950) as phytotoxic air pollutants. The available diagnostic methods are described in 3.1; therefore, only a few additions are necessary.

Since the successful studies on the etiology of a widely-occurring new type of injury on cultivated plants in California during the 40's and 50's, sporadic and systematic attempts have been made to determine the intensity and spatial distribution of the injury. Acute injury on oxidant-sensitive plants such as tobacco, grape, lettuce, bean, or potato is comparatively simple and reliable to monitor by establishing the degree of necrosis. By 1955, a monitoring program was established covering all of California using agricultural crops, fruit trees, flowers, and native weed species (Middleton and Paulus, 1956) (compare Section 2.5.3). Computer analysis was used to determine areas of differential exposure. However, difficulties exist in the determination of impacts from chronic exposures, such as growth losses, reduction in fruit and flower formation, and reduced yield and quality in agriculture. When large areas are impacted, it is only possible to only approximate the suspected injurious agent because of differences in external growth factors.

In forest ecosystems, monitoring has concentrated on determining the injury on the dominant tree species, for example, ponderosa pine in California and eastern white pine in the eastern United States. Suitable criteria to establish the health of conifers include the amount of needle retention and their condition; studies on the height and radial growth of trees allow the reliable determination of growth losses to forestry (Pollanschütz, 1975). Dendrochronological investigations permit conclusions about the pollutant exposures during the past years and decades.

Large scale monitoring of air pollutant-impacted forest stands has been accomplished using false-color photography (Wert et al., 1970). A scale of 1:8,000 is suitable for groups of trees, and at 1:584, injury can be recognized on individual trees. For example, photochemical oxidant injury in the Los Angeles and San Bernardino National Forests covered 40000 ha and affected approximately 1.3 million trees. The evaluation of risks to forest trees is also possible by determining the condition of visibly injured native, non-tree species. The common milkweed (Asclepias spp.) that is widely distributed in North America has been proposed for this use (Duchelle et al., 1980) because it has been shown to be very susceptible to ozone in both open-top chambers and in field studies. The presentation here has been brief because this same theme has been extensively discussed in other publications (e.g., see Heck and Brandt, 1977).

3.2.1.1.2 Synecological Procedures

Because of the limited studies concerning the effects of air pollutants on ecosystems (see Chapter 2.5), the interactions of plant associations has not attained any significant importance as a bioindicator.

For plant communities to be suitable indicators of air pollutants, two questions are decisive: what requirements are needed to reliably establish pollution-induced changes in plant communities; and how sensitive are plant communities in comparison to their individual species? At present, it is not possible to answer to either question with practical experiences or experimental results from comparative studies. The sensitivity of plant communities in comparison to their individual member species can be deduced from the type and manner by which alterations in plant communities occur. The mechanisms of air pollution-induced alterations are based on:

- the variable magnitude of effects on differentially susceptible community members;
- pollution-dependent changes in the interspecific competitive conditions; and
- the secondary succession processes induced by air pollution.

Pollution-induced shifts in the interspecific competitive relationships can impair the more susceptible plant species of a community and thus increase the direct damage to those community members. Moreover, alterations in interspecific competitive conditions may occur at such low concentrations that the individual species of the community are not injured but produce stimulatory effects that can give a competitive advantage to specific plant species (Guderian, 1978). Accordingly, one can see that specific associations of higher plants may be more sensitive indicators of phytotoxic air pollutants than the individual species comprising them, as has been observed in the initial studies on this topic.

The greater sensitivity of plant communities compared to the corresponding homotypic populations does not necessarily mean that they are better bioindicators. For this characteristic, it is more important to know how large the change and what efforts must be used to reliably detect pollution-induced shifts under typical conditions. Finally, the significance of plant communities as indicators of air pollution will depend on the results obtained from exposing specific model plant communities (Küppers, 1984) and from determining chronic effects under natural conditions using permanent sample plots (BMI, 1978).

Alterations in structure and composition are useful indicators of pollutant effects on plant communities. Using plant sociological mapping techiques, zones of differential impact can be established. Depending on the type and concentration of exposure, some species are aggregated, others uniformly distributed or completely absent (Niklfeld, 1978; Trautmann et al., 1971; Wedeck, 1980). In this context, Hajdúk (1961) used the terms "positive" and "negative" phytoindicators, while Anderson (1966) used the terms "increaser" and "decreaser." These results were obtained around individual sources emitting primary air pollutants with sharp gradients in ambient concentrations and damage responses. Given the large areas impacted with photochemical oxidants which display similar amounts of injury, the conditions are naturally less favorable for the establishment of pollution-induced changes in plant communities and the use of these changes as bioindicators. During the last several years, efforts to determine air pollution-induced changes in plant communities (Taylor, 1974a; Williams et al., 1977; Westman, 1979; Smith, 1980; Blum et al., 1980; Montes et al., 1982) have increased the possibility that such changes can be used to recognize oxidant impacts, particularly to establish the extent of damage according to the intensity and spatial distribution.

3.2.1.2 Active Monitoring

Responses of native and cultivated plants growing in their habitats serve, as described in Section 3.2.1.1, primarily to establish the causes of pollutant-dependent injury and determine their spatial distribution. These characteristics are less suited for the quantification of air pollution impacts or for monitoring of pollutant effects. The plant material itself is too heterogeneous and the climatic and soil conditions are too variable to permit valid comparisons. Two approaches have been used to overcome these difficulties: standardized plant culture and the exposure of standardized plants using special methods.

3.2.1.2.1 Standardized Plant Culture

The quality of biological measurements, as with physical-chemical methods, depends heavily on the reproducibility of the test results. Consequently, one should try to minimize the variability caused by external and internal factors associated with a pollutant exposure.

The standardization of plant culture produces a narrowing of the spectrum of effective factors and thereby a reduction in experimental variation. Concurrently this approach can be used to significantly control and reproduce the conditions that influence pollutant uptake and pollutant effect. Methodological helps for plant culture under similar conditions include the use of high value seeds, the standardization of seeding, plant culture and growth conditions such as soil, water, and nutrient supply.

A classic example of a standardized procedure for plant culture and exposure is the protocol for the ozone-sensitive tobacco cultivar Bel W3 developed by Heck et al. (1969). Since then, this method has been used successfully in the USA and other countries as a bioindicator for photochemical oxidants (compare 3.2.2). To determine the effects of primary air pollutants, especially compounds that are accumulated in the plant, the grass culture procedure developed by Scholl (1971) has been useful, particularly as an "accumulation-indicator." The culture and exposure of Italian ryegrass (Lolium multiflorum) as an indicator plant including the sampling and analysis are detailed in VDI-Richtlinien 3972, B11 (VDI, 1978) and 3792,B1.2 (VDI, 1982).

3.2.1.2.2 Exposure Systems

When using plants as air pollution indicators to establish the nature and level of the current exposures, optimal results are obtained only when the plant culture and exposure methods are standardized. One can select between exposures in containers or field plots in the ambient air or exposure systems with and without air filtration. The culture of indicator plants in plots receiving ambient air such as the "Test Plant Procedure" (Schönbeck, 1963) or "Test Plot" (Spierings, 1967) has practical significance for the study of primary air pollutants. Comparable studies with photochemical oxidants are not known. In contrast, the container-culturing of bioindicators has achieved a greater significance, as illustrated by examples in 3.2.2, particularly the protocol of Heck et al. (1969). Above all, with the typically large areas impacted by photochemical oxidants, it is very difficult to reliably determine the intensity and spatial distribution of the pollutant effects because air pollution-induced changes are frequently small compard to the variation in plant growth induced by soil and climatic conditions. Comparative studies at the same site with indicator plants in exposure systems with and without air filtration make it possible to reliably detect the extent of plant impacts from moderate exposures. Currently available methods to determine air pollution effects on plants and their particular applications are described in greater detail in Section 3.4.

3.2.2 Bioindicator Results from Various Countries

Plants have been used as bioindicators for photochemical oxidants in both in North America and other parts of the world using various active monitoring methods (3.2.1.2). A few examples of the data obtained will illustrate the feasibility and limitations of the methods.

The bioindicator methods developed by Heck _et al_. (1969) were used to monitor the occurrence of ozone injury on Bel W3 tobacco in the vicinity around Cincinnati, Ohio, USA (Heck and Heagle, 1978). The injury intensity varied among the years --1966 to 1968 -- but was correlated with the weekly mean ozone concentrations as influenced by various external factors. Craker _et al_. (1974) also used the methods developed by Heck _et al_. (1969) when they exposed Bel W3 tobacco in the vicinity of Sudbury, Massachusetts. Based on the amounts of foliar necrosis on tobacco leaves, lines of equal injury intensity, "Isopollutans," were developed. The results from sites covering the state of Massachusetts showed that this method was suitable for distinguishing zones of differential exposure (Jacobson and Feder, 1974). Kelleher and Feder (1978) were able to show, with the help of Bel W3, the long distance transport of photochemical oxidants. On Nantucket Island in the Atlantic Ocean, 340 km east-northeast from New York, photochemical oxidant injury occurred on tobacco plants primarily when the winds were west-southwest, from densely populated areas. Measured ambient ozone concentrations were in good agreement with the bioindicator results.

Outside of North America, Knabe et al. (1973) exposed various tobacco cultivars during 1967 and 1968 using the procedures of Heck et al. (1969) at four pollutant-impacted sites in the German Federal Republic. In 1963, E. F. Darley (unpublished data) established that both ozone and PAN symptoms occurred on native plants growing in the Ruhr area. The extent of foliar necrosis on experimental tobacco plants at the various sites showed that photochemical oxidants were a widely distributed type of air pollution in the Federal Republic of Germany. Foliar injury also occurred at a "clean air station"in southern Westphalia, but the extent of injury was less than at stations in the industrial areas. Since then, results from both local and regional studies, for example Cologne and western Ruhr (Scholl and van Haut, 1977), Munich (Rudolph, 1977a, 1977b), the lower Main region (Steubing, 1977, 1980), and Stuttgart (Rabe, 1978; Arndt and Lindner, 1981) have confirmed the widespread occurrence of phytotoxic concentrations of photochemical oxidants.

Bioindicator plants have been used with good results in Great Britain. In 1972, Bell and Cox (1975) exposed three tobacco cultivars (Bel W3, Bel B, Bel C) at sites to the west of London. They found that, with distance, Bel W3 reacted the most sensitive. The degree of foliar necrosis on Bel W3 correlated closely with the number of hours that the ozone concentration equaled or exceeded 0.04 ppm. Ashmore et al. (1978) exposed tobacco plants throughout all of Great Britain and confirmed the wide scale distribution of photochemical oxidants. The assumption of Bell and Cox (1975) that the current oxidant exposures were injuring not only highly sensitive indicator plants but also agricultural plants has been confirmed (Ashmore _et_ _al_., 1980b). They used open-top chambers (Mandl _et_ _al_., 1973). and exposed various radish and pea cultivars at the same locations used in the study of Bell and Cox (1975). Considerable foliar necrosis occurred on ozone-sensitive pea cultivars, while radish cotyledons were chlorotic and abscised prematurely. Measured ozone concentrations with peak values to 0.14 ppm were phytotoxic to sensitive plant species. Injury on corn and tomatoes in the vicinity of the exposure site could not definitely be ascribed to photochemical oxidants because of the lack of standardization.

Photochemical oxidant-induced plant injury has been observed in The Netherlands since 1965 (ten Houten, 1966). Typical PAN symptoms were observed on native plants, annual bluegrass, little leaf nettle (Urtica urens), and nettleleaf goosefoot (Chenopodium murale), in the vicinity of an oil refinery center. The concurrent exposure of indicator plants, tobacco (Nicotiana rustica), spinach, lettuce, and several chrysanthemum cultivars under standard conditions confirmed the occurrence of PAN. A country-wide monitoring network has been established in The Netherlands since 1969 and, with the aid of chemical-physical methods, determined the primary and secondary substances of photochemical smog (Guicherit, 1975). In parallel, exposures of oxidant-sensitive plants has occurred since 1973 (Posthumus, 1976). The bioindicator plants and the observed symptoms are listed in Table 4. The plants were exposed for weekly periods and then evaluated. The greatest photochemical oxidant exposures occurred around Rotterdam (Floor and Posthumus, 1977).

Also, in other European countries, the first indication of photochemical oxidants resulted from the use of the bioindicator, Bel W3 tobacco. Ozone effects were demonstrated not only in Switzerland, France,

Table 4. Indicator plants for monitoring photochemical oxidants in The Netherlands (Posthumus, 1976).

Plant species and cultivar	Symptoms	Pollutant
Little Leaf Nettle	leaf undersurface bronzing (band form)	PAN
Annual Bluegrass	bifacial leaf necrosis (band form)	PAN
Tobacco cv. Bel W3	necrotic flecks (spots) on the upper leaf surface	O_3
Spinach cv. Subito cv. Dynamo	necrosis on the upper leaf surface	O_3

and Belgium, but also in the northern European countries of Denmark and Sweden (Eastmond and Skärby, 1979; Ro-Paulsen et al., 1981). The Swedish investigations produced the hypothesis that photochemical oxidants resulted from both local sources and long distance transport to the monitoring sites (Skärby, 1979).

In the subtropical climate of Israel, the bioindicator Bel W3 can be used in either the field or in chamber exposure systems with or without air filtration during the winter months (Goren and Donagi, 1980). However, during the summer months the closed exposure chambers could not be used because of overheating (Naveh et al., 1978). They found a good correlation between the extent of foliar injury and the ambient oxidant concentration.

Active and passive monitoring programs using bioindicators have been used in Japan since 1973 (Matsunaka, 1973; Shiratori, 1973). Buckwheat and oak are grown under standardized conditions in containers and exposed at the study area. Concurrently, injury symptoms on pines (Pinus thunbergii and Pinus densiflora) and cultivated vegetable species, onion, radish, morning glory, black radish, and taro, growing in the study area are evaluated. Foliar injury serves as the response criteria. Since then, the response of morning glory to photochemical oxidants in both controlled exposures and field studies has been calibrated so that the intensity of the plant reaction can be used to infer the mean ozone concentration during the exposure period (Nouchi and Aoki, 1979).

3.2.3 Comparison of Biological and Physical-Chemical Methods

When sensitivity, specificity, and reproducibility are used as criteria to evaluate measurement methods, comparison generally favors the physical-chemical ones; typically they are more sensitive, specific, and reproducible than biological methods. Also, physical-chemical methods permit the exact determination of the concentration-time profile. With this assumption and in view of the significant progress recently made in physical and chemical methods for air analysis, it seems difficult to understand the growing use of biological methods in environmental protection (Jacobson, 1977b; Floor and Posthumus, 1977; Prinz and Scholl, 1978; Arndt et al., 1982a).

An explanation of this apparent contradiction results from a comparison of the expected results from physical-chemical and biological methods (Guderian and Reidl, 1982) and emanates from the specific data needs for individual environmental protection measures (Table 5). In this respect, it should be remembered that the quantitative responses of biological objectives are not to be understood in the same sense as classical physical measurements (Schönbeck and van Haut, 1971). An absolute causality, where the same cause always has the same effect, is not detectable. In its place are statistical occurrences regulated by the laws of probability which make possible the successful use of plants as indicators of biologically active air contaminants.

The primary goal of environmental protection is not to reduce emissions or ambient concentrations but to protect humans, animals, plants, and materials from injurious environmental effects. However, that does not mean that the determination of effects alone is a sufficient or optimal information base. If specific air pollution effects are to be prevented, it follows that emissions must be restricted to a given quantity through the establishment of emission standards that are monitored by chemical-physical methods. The same is true for ambient air standards. Ambient air standards provide a possibility for prophylactic environmental protection

Table 5. Uses and limitations of physical-chemical and biological methods for the determination and evaluation of pollution impacts (Guderian and Reidl, 1982).

Physical-Chemical Methods	Biological Methods
Quantitative measurement of individual atmospheric components	No measurement in the physical-chemical sense; evaluation of air pollution exposure through numerous nonspecific reactions
Monitoring of emission and ambient air quality standards	Response thresholds possess a high relevance because air pollution legislation has the goal of reducing specific effects
No determination of effect or risk evaluation	Determination of actually occurring effects in the form of injury and pollutant enrichment at various organizational levels, an indicator of disruption in the ecosystem
Risk prognoses are possibly only for individual components	Evaluation of the total exposure, possibility of determining joint effects
The active portion of a mixture of air pollutants can frequently be only approximated	The effects reflect the active portion of the pollutant mixture
Determine emissions and ambient concentrations at a specific time (characterization of concentration-time profile)	Expression of effects during a specific time period; determination of effects on perennial plants

(Prinz and Scholl, 1978), an essential condition particularly for the protection of humans. With biological indicators, however, only those exposures that are already in the toxic range can be determined.

The measurements of emissions and ambient concentrations cannot replace the determination of biological effects and the biological effects cannot replace the chemical-physical measurements. The comparison (Table 5) of the specific use of physical-chemical and biological methods is applicable not only the effects of photochemical oxidants but gaseous air pollutants in general. Moreover, it should be remembered that with such different materials, gross simplification is required.

The primary value of biological indicators lies in their expression of effects and indication of the phytotoxic components currently in the ecosystem. Bioindicators permit the evaluation of the total exposure; they react with only the biologically active components of the atmosphere and permits the reliable prognosis of risks for other components in the ecosystem (Guderian and Reidl, 1982). When one be considers that information from biological indicators is frequently obtained with comparatively small expenditures (Claussen, 1980), their increased use is understandable. According to the nature of the question, physical-chemical or biological methods may be used. As a whole, a meaningful combination of both response systems provides an optimal information basis for the prompt recognition and control of air pollutant-induced risks.

3.2.4 Conclusions for the Use of Bioindicators

Bioindicators, with their ability to evaluate the extent of effects from current exposures and to predict future risks, can be used with the following objectives:

- -- recognition of causes of plant injury;
- -- delimitation of exposed areas and gradation of exposure levels with temporal relationships;
- -- risk prognosis for agriculture, horticulture, and forestry land uses;
- -- evaluation of risks to semi-natural ecosystems;
- -- optimal spatial planning based on environmental protection requirements;
- -- determination of air quality criteria;
- -- surveillance of permissible ambient concentrations; and
- -- demonstration of the effects of photochemical oxidants.

If and to what extent higher plants maintain or increase their role as air pollution indicators for environmental protection depends when and with what success the following points are considered in conducting the the corresponding research:

1. Greater consideration should be given to the selection of indicator organisms, based on the ecological performance of vegetation.
2. The selection of air pollution indicators should specifically consider the chronic effects of low concentrations of complex pollution types.
3. The increased use of homo- and heterotypical populations for active monitoring, particularly exposure systems with and without air filtration is encouraged, to determine the type, intensity, and spatial distribution of chronic, low level exposures.
4. Comparative studies of homo- and heterotypic populations should clarify if, and to what extent, plant communities are more

sensitive than the individual species composing them. Studies to determine air pollution-dependent risk to plant communities should be conducted through:

- -- development of experimental conditions and of intensive epidemiological studies to determine the effects on highly structured systems;
- -- establishment of permanent plots for successional controls; and
- -- studies of the characteristics of model plant communities or portions of ecosystems as indicators for ecotoxicological tests.

5. Work to standardize the culture and exposure of plants suitable as bioindicators should be intensified.
6. Comparative studies should clarify the extent that specific reactions of air pollution indicators can be used to reliably determine the consequences of risk to other plants or other components in the ecosystem.

3.3 Classification and Evaluation of Effects

In determining and evaluating air pollutant impacts on plants, its effects on various ecosystem functions should also be considered (Figure 1). Above a specific threshold, air pollution will impair or eliminate the performance of vegetation, i.e., as a primary producer, as an economic objective, as a component of a healthy ecosystem and environment, and as a gene reservoir. To use this reduced vegetation performance as a basis for remedial or mitigative action, criteria must be selected that evaluate the usefulness of individual plants and vegetation as a whole from ecological and economical viewpoints. For the various effects of air pollutants at the individual organizational levels of the ecosystem, Vogl et al. (1965) and Weinstein and McCune (1971) developed a classification system, without consideration of the relationship of the response to the useful value of the plant. This concept was used to categorize (Table 6) the effects of photochemical oxidants described in Chapter 2.

3.3.1 Classification of Effects

At the cell, the lowest organizational level of the ecosystem, effects are initially expressed as altered permeability of biomembranes causing changes in cellular compartmentalization, water and mineral relations. These impacts, as well as changes in enzyme activities, altered metabolism, changes in cellular structure and organization, including fine structure changes, cause cellular perturbations and/or cell-death.

Cellular changes above a specified magnitude influence the next higher organizational level, for example, through reduced photosynthesis rates, elevated respiration, or disruption of plant water relations. A reduced CO_2 assimilation rate affects leaves and frequently processes in other plant organs, especially root growth (Tingey, 1977; Oshima et al., 1979), rhizobium induced nodulation of legumes (Manning et al., 1971; Tingey and Blum, 1973; Tingey, 1977), and the development of mycorrhizae on specific tree species (Parmeter et al., 1962; Miller, 1973a) as a consequence of altered metabolite partitioning. Foliar injury symptoms include pigmentation, chlorosis, and necrosis, and they are frequently coupled with increased chlorophyll decomposition. It should be remembered that foliar injury does not always result in reduced growth or yield and also that growth and yield can be reduced without the accompanying visible symptoms

Table 6. Classification of Photochemical Oxidant Effects on Plants

Organizational Level			
Cell	Tissue	Organism	Community
Increased membrane permeability	Changes in photosynthesis, respiration, and transpiration	Changes in plant growth	Reduced plant growth and productivity
	Alterations in the partitioning of metabolites		Fluctuations in composition and reduction in species abundance
Altered enzyme activities	Alterations in growth and development of individual organs	Increased susceptibility to biotic and abiotic stresses	Changes in stand structure
Increased stress ethylene production	Pigmentation, bleaching, and chlorosis	Disturbances in fruit production	Distruption of food chain
			Changes in plant succession
			Possible changes in nutrient cycling
			Risks to consumers and decomposers
Ultrastructural changes in organelle	Necrosis	Reduced yield and quality	Impairment of ecosystem productivity, including its stability and capacity for self-regulation
Changes in cellular metabolism			
Altered cellular structure	Reduction in rhizobium induced nodulation	Altered plant competitive ability	
Disrupted cellular functions	Disturbance of mycorrhizal development	Death of plants	
Cell death	Death or loss of plant organs		

(see 3.1.2). Reduced pollen production and altered pollen tube growth (Feder, 1968) can lead to reduced fruit production. At this level of organization the most severe effects include the premature senescence, death, and casting of plant organs.

Effects on cells and organs affect organismal growth, which includes not only "system synthesis" but "product synthesis," i.e., the development of such organs which are harvested will be affected and this will in turn affect yield. In addition to "primary" effects, "secondary" ones (Donaubauer, 1966; Heagle, 1973; Laurence, 1981), can result from reduced plant resistance to biotic and abiotic factors with consequences that can approach complete yield loss and reduced quality.

The composition and species abundance in plant communities may change as a result of various direct effects on individual, differentially susceptible plant species. Pollutant-induced changes in interspecific competitive conditions and secondary succession may also occur (Guderian and Küppers, 1980b). These effects and changes in stand structure, may also endanger consumers and decomposers (Miller and White, 1977). In the final result, the productivity of the ecosystem including its stability and capacity for self-regulation are impaired (see 2.5).

3.3.2 Evaluation of Effects

The briefly described effects on plants at the individual organizational levels of the ecosystem have different values for evaluating the effects of air pollutants on the useful value of plants (Guderian *et al*., 1960). The segregation of air pollutant-induced reactions into "injury" and "damage" is now widely used in studies to evaluate air pollution effects (Brandt, 1962; Heggestad and Heck, 1971; NATO/CCMS, 1974; Tingey *et* al., 1979). Such a classification permits comparison of effects on different plant species.

Injury encompasses all plant reactions such as reversible changes in metabolism, reduced photosynthesis, leaf necrosis, leaf drop, altered quality or reduced growth that do not influence yield. Damage includes all effects that reduce the intended use or value of the plant (Table 7). These useful values, characterized by economic production, ecological functions, ideal values, and vegetation as a gene pool, can be reduced through the direct impact of air pollutants. Numerous studies describe this "primary damage." In contrast, there is little information concerning "secondary damage" as a consequence of photochemical oxidant reduced resistance to biotic and abiotic stresses (Taylor, 1973a, 1973b; Heck et al., 1977b).

The economic damage to agriculture, forestry, and horticulture results from direct impacts on plants, including primary and secondary damage, and indirectly through changes in farming and cultural practices. The estimation of direct economic damage includes effects of growth, yield, and quality -- in part a subjective value. Products used as food, fodder, or ornamental plants may show quantitative and qualitative losses ranging from changes in the composition of nutritional metabolites (Feder, 1977; Neely et al., 1977; Pell et al., 1979) that influence production value to impaired appearance. In addition, impacts on seed quality and alteration in pollination in forests will have lasting effects on natural reproduction. Additional information on these facets of damage is contained in Section 2.5.

Economic losses may also occur because plant species especially adapted for cultivation in specific locations can no longer be grown

Table 7. Effects of Photochemical Oxidants Exposure on the Performance on Plants in Ecosystems

INJURY
All Reactions of Air Pollutants

DAMAGE
Effects on Useful Value

Primary Damage			Secondary Damage	
Economic Performance		Ecological Functions	Ideal Value	Genetic Resources
Direct	Indirect			
Growth and yield reductions	Reduced selection of plant species, changes in cultivar selections and cultural practices	Reduction in the areal functions of of vegetation	Reduction of scientific, ethical and aesthetic value	Gene erosion through reduced abundance distribution or loss of plant species and ecotypes
Reduced quality of foodstuffs, fodder, raw materials, and ornamental plants		Stabilization of water relations and climatic regulation		
	Increased expenditures for cultural and maintenance needs	Nutrient cycling		Reduction of genetic resources for breeding purposes
Impaired seed production and plant quality		Reduction of soil erosion requirements		
		Reduction of noise and air pollution		
		Welfare effects		

because of their pollutant sensitivity. The necessity of cultivating relatively resistant species may cause changes in management or cultural practices that may impart considerable disadvantages to crop production. Frequently, additional expenditures for cultural measures can cause additional financial costs. These primary and secondary damages to agricultural, horticultural, and forestry plants frequently have economic consequences for the individual producer and at the national level (Jacobson, 1982).

The ecological value of vegetation results from its function as a component of a healthy habitat, both agricultural and recreational, and to its contributions to the maintenance of water and climatic conditions and its role in reducing erosion (water and wind), air pollution and noise. Photochemical oxidants may disrupt these ecological functions over large areas, for example, various regions of the USA are already impacted, as shown by Westman (1977) for example in his evaluation of "non-monetary costs" of pollution to ecosystems (see Section 2.5.4 for additional details).

Photochemical oxidants occurring over large areas can cause injury symptoms on ornamental plants in parks and gardens (Feder, 1970a). The reduced ideal and esthetic values of this vegetation frequently results in complaints based primarily on visible appearance rather than effects on growth. Air pollution effects on ecological and ideal values of vegetation must be considered in relation to the World Health Organization definition of human health, which includes not only freedom from disease but also the well-being of man.

Most investigations of oxidant effects on plants have concentrated on economically important species (Manning and Feder, 1976; Linzon _et_ _al_., 1975; Heck et al., 1977b). For these plants, at least in the United States, criteria to evaluate of effects and response thresholds have been developed (Chapters 2.5, 4.1, and 6). However, it is not clear what levels of chronic pollutant doses may occur before inducing gene erosion (Scholz, 1980, 1981) through the redcued distribution, abundance, or death of individual species. In his studies of the coastal sage scrub community of the southern California coast, Westman (1979) showed that photochemical oxidants caused a reduction in number of species and cover of the native vegetation. Native species represent an important gene reservoir useful in the breeding of agricultural plants. This natural variation of genetic material is essential to assure continued food production aside from the consideration of other concerns such as scientific, ecological, ethical, and esthetic interests.

3.4 Experimental Approaches to Determine Air Pollution Effects

The methods for determining air pollution effects are as diverse as the participating disciplines. The standard approaches of air monitoring, exposure methods, statistics, as well as various biological and physical sciences, provide the tools for the diagnosis and evaluation of air pollution effects. Air pollutants and their effects on various organizational levels of ecosystems display various particularities that have led to the development and use of additional specific experimental designs and equipment. Obviously, these methods are topics for discussion but it is not the purpose of this section to describe the specifics of individual methods. This information can be found in the original publications as well as in recent literature reviews on the topic (e.g., Ormrod, 1978; Heagle and Philbeck, 1978; Heagle et al., 1979d). Rather, this presentation will attempt to describe the criteria to use in the selection of experimental methods. Two factors should be noted: (i) the risk of selecting the wrong or non-optimal methods to evaluate the experimental hypothesis; and (ii) that by an evaluation of the data developed from these selected methods the investigator failed one to recognize its limitations for a particular experiment or epidemiological survey.

3.4.1 Criteria for Selecting Experimental Methods

The selection of experimental methods to study the effects of air pollutants on plants depends primarily on the hypothesis and secondarily on the parameters used to determine the effect.

In the present context, the total plant response to air pollutants can be subdivided into the determination of the:

- cause of injury;
- type, intensity, and spatial distribution of the injury;
- quantitative relationships between exposure and response;
- basis of mitigative actions in the field;
- mode of action of individual components, singly and in combination, in a pollutant complex.

Each of these complex questions encompasses a variety of specific questions (see Sections 2.5, 3.1, 4.1, 4.3.2, 4.4, and 6). It is obvious that to find answers to these questions, different approaches, i.e., various experimental methods, are required. Soil and climate as external factors (Section 4.2) and developmental stages and leaf age as internal factors (Section 4.3) significantly influence a given pollutant exposure. Recent comparative studies with bush beans (Lewis and Brennan, 1977; Beckerson _et al_., 1979; Meiners and Heggestad, 1979) and potatoes (Reinert, 1980) demonstrate that plants react differentially to ozone, depending on whether they were cultivated in closed chambers or the field. This is particularly true for the quantitative relations between exposure and effect, and seldom or never for the quality of the effect. Also, the experimental object, itself significantly influences the experimental approach (see Section 3.4.2.1). In the final analysis, the main concern is the determination of air pollutant-induced deviations from the norm at individual organizational levels of ecosystems. The study of pollutant effects, at least from the perspective of practical environmental protection, is not an end in itself, but provides the basis for mitigative actions. Therefore, the norm is the plants or plant communities as they occur in agrarian (agriculture, horticulture, and forestry) and natural ecosystems. The following discussion is on experimental methods which can be used to evaluate air pollution effects on plants in their habitat. Results from studies with plants cultured in typical conditions, are representative for practical exposure relationships. However, representativeness is only one basic requirements to insure quality of results. In general, the cause-effect relationship must be established as well as quantifying the effect (Sections 4.1 and 6).

The three basic requirements needed to reach a conclusion are: representativeness of typical conditions, assurance of cause-effects associations, and quantification of exposure-response relationships. These require the use of different experimental methods. The material in the following scheme will be used to discuss and illustrate the experimental approaches best suited for each experimental question as well as those which are less suited.

Moving from top to bottom, Table 8 is divided into three sections to illustrate types of exposure relationships. Photochemical oxidant pollution is a complex of pollutants composed of ozone, peroxides and other oxidants, in addition to the precursors of these secondary products. Because photochemical oxidants have wide spatial distribution, they are frequently associated with primary pollutants such as sulfur dioxide or gaseous fluoride. In addition to the complex composition, one must accept fluctuations in the exposure characteristics, concentration, and duration. In gaseous exposure studies, the exposure of each component including concentration, duration, and frequency of affect can be controlled at any arbitrary level. When studying the effects of primary components under actual or typical conditions, the possibility exists to evaluate the effects of a specific air pollutant component through the choice of a suitable emission source.

The various environmental conditions (Table 8) include edaphic, climatic, and organismal, as well as their interactions. In this context, the term natural means conditions as they occur in natural ecosystems; semi-natural implies conditions such as occur in managed forests, and other managed systems such as agriculture and horticulture. The influence of the experimental systems used to determine exposure response in semi-natural and managed systems can induce detrimental deviations from the natural conditions. Controlled conditions, as found in controlled-environment facilities, permit the regulation of the pollutant exposure as well as the growth parameters. Experimental studies on managed, semi-natural, and natural associations must consider the varying environmental conditions and in some studies a varying pollutant exposure.

Table 8. Methods for determining effects of air pollutants (adapted from Guderian, 1978).

Exposure Characteristics	Various Environmental Conditions			
	Controlled	Managed Systems	Semi-natural	Natural
Complex pollutant exposure as in areas subjected to photochemical oxidants.			Studies on plants in open-top chambers and plots with and without air filtration plus pollutant addition.	Geo-biological studies in agricultural and natural ecosystems.
Pollutant exposure can be selected especially in the vicinity of a source emitting primary pollutants.			Studies on plants in open-top chambers and plots with and without air filtration plus pollutant addition.	Geo-biological studies in agricultural and natural ecosystems.
Pollutant concentration and exposure duration are controlled.	Pollutant exposures in controlled-environment rooms.	Pollutant exposures in greenhouses.	Pollutant exposure: open-top chambers, linear-gradient chambers, Zonal Air Pollution System (ZAPS).	
			Computer controlled exposure system.	

↑ Increasing difficulty in establishing cause-effect and quantifying exposure response.

Increasing difficulty in extrapolating experimental results to the field.
←

3.4.2 Experimental Procedures

The following discussion will use the classification in Table 8 in an attempt to illustrate the limits of the experimental procedures used to determine air pollution effects in natural, semi-natural, managed, and controlled systems.

3.4.2.1 Studies Under Natural Conditions

Geobiological studies are conducted under natural conditions and the experimental procedures should not influence the environmental conditions. These studies can be conducted in the vicinity of a pollution source as well as in large areas impacted by pollution. In studies near a pollution source, the exposure is characterized by the presence of one or only a few components, and there is typically a distinct decrease in the concentration frequency with distance from the source, unless there is an elevated background and a high frequency of pollution-free periods during the total exposure period (Guderian and Stratmann, 1962, 1968). Given the limited extent of the experimental area, one would expect only small differences in environmental conditions so that prerequisites would be generally favorable for evaluating local impacts of the air pollutant(s).

In congested areas with a high density of emission sources and also in areas impacted by photochemical oxidants, numerous biologically active components can co-occur. In general, the pollutant concentrations display only a gradual decline with distance from the emissions area. However, the mean photochemical oxidant concentrations may be higher away from the congested areas than near the source, where the precursors are emitted (see 1.3.2.2). The pollution-induced reductions in plant production also exhibit only small changes with distance from the emissions area. Comparisons with unexposed locations (controls) are possible only at substantial distances from the experimental plots which can experience a wide range in conditions between test and control locations. These differences, depending on the research subject, may cause significant problems in drawing inferences about the variations in plant performance at various locations from the source.

Forest stands provide relatively favorable conditions for quantifying pollution-induced effects. On the basis of experimental values and yield tables, the number of injured and dead trees in a stand or the evaluation of height and radial growth can provide a reliable estimate of air pollution impacts (Miller, 1973a; Taylor, 1973b; Miller and White, 1977). Chronological studies of the annual growth rings can evaluate growth disturbances that occurred in past years and decades. Another example of the geobiological approach is Westman's study (1977) in which he associated changes in the composition of coastal sage scrub in the southern California coastal area to a gradient in ozone exposure. With agricultural and horticultural plant species, geobiological studies provide estimates of yield losses from photochemical oxidants through the use of pot-culture techniques. The O_3 concentration gradients in the Los Angeles basin have been used in estimating the influence of ozone dose on the yield of tomato (Oshima _et al_., 1975) and alfalfa (Oshima _et al_., 1976). Regression analyses indicated that differences in temperature and humidity at the different sites had less effect on crop yield than did the difference in ozone dose. However, in this case only the pollutant-exposure conditions can be considered natural, not the growth conditions of the experimental plants.

In summary, geobiological studies can quantify the long-term effects of pollutants on homo- and heterotypic populations under typical interplant competitive and environmental conditions. Vegetative studies, particularly on floristic systems, can provide information about changes in species numbers and species association. Finally, geobiological studies provide a representative basis for evaluating the reaction of other components (consumers and decomposer) in the ecosystem (compare Sections 2.5.3.2 and 2.5.3.3). Geobiological studies are not appropriate for determining photochemical oxidant-induced yield reductions in agriculture and horticultural cropping systems. Gradations in injury intensity can be established by evaluating external injury symptoms. Difficulties in recognizing the particular phytotoxic components and accurately characterizing the exposure, limit the broader use of this method, as does its substantial cost.

3.4.2.2 Studies Under Semi-natural Conditions

In contrast to geobiological studies under natural conditions, studies in semi-natural conditions use various experimental aids that may influence the plant environment. According to the definition, we are discussing studies in semi-natural conditions, where the experimental apparatus will have minimal influence on the plant reaction to the air pollutant. Special efforts are made to ensure that the experimental conditions approach a natural situation, where at most the plants are laterally enclosed with a transparent film which is open at the top so they are exposed to the atmosphere. In contrast to closed chambers typically used in controlled-environment chambers and greenhouses, the "greenhouse effect" producing elevated temperatures and altered light quality does not occur.

This method is characterized by the use of a series of similar systems, at a given location, under semi-natural conditions in which the systems receive:

air with filtration;

air without filtration; and

air with pollutant addition with or without air filtration.

The motivation for developing these systems was: i) the difficulty in extrapolating experimental results for controlled-environment or greenhouse studies to typical field conditions; and ii) the difficulties associated with studies in natural conditions in establishing cause and effect and the problem of establishing the relationship between exposure and response (Heagle et al., 1979d; Heck et al., 1982). Four examples will illustrate the uses and limitations of these methods.

3.4.2.2.1 Open-Top Chambers

During the early 1970s, concurrent research at Boyce Thompson Institute for Plant Research (Mandl et al., 1973) and U.S. Environmental Protection Agency/U.S. Department of Agriculture (Heagle et al., 1973) developed open-top chambers as a new experimental method which had significant advantages over closed-chamber and open-atmosphere approaches for evaluating air pollution exposures and their effects (Figure 9). Both open-top chamber designs were cylindrical (diameter 2.16 to 3.05 m), about 2.4 m high and covered with either corrugated fiber glass panels or clear polyvinyl chloride film. The two designs displayed some differences in the air filtration, air handling systems and the frequency of air exchange (Heagle and Philbeck, 1978), however, the performance of the chambers was similar. The chamber can use either filtered or unfiltered air which is

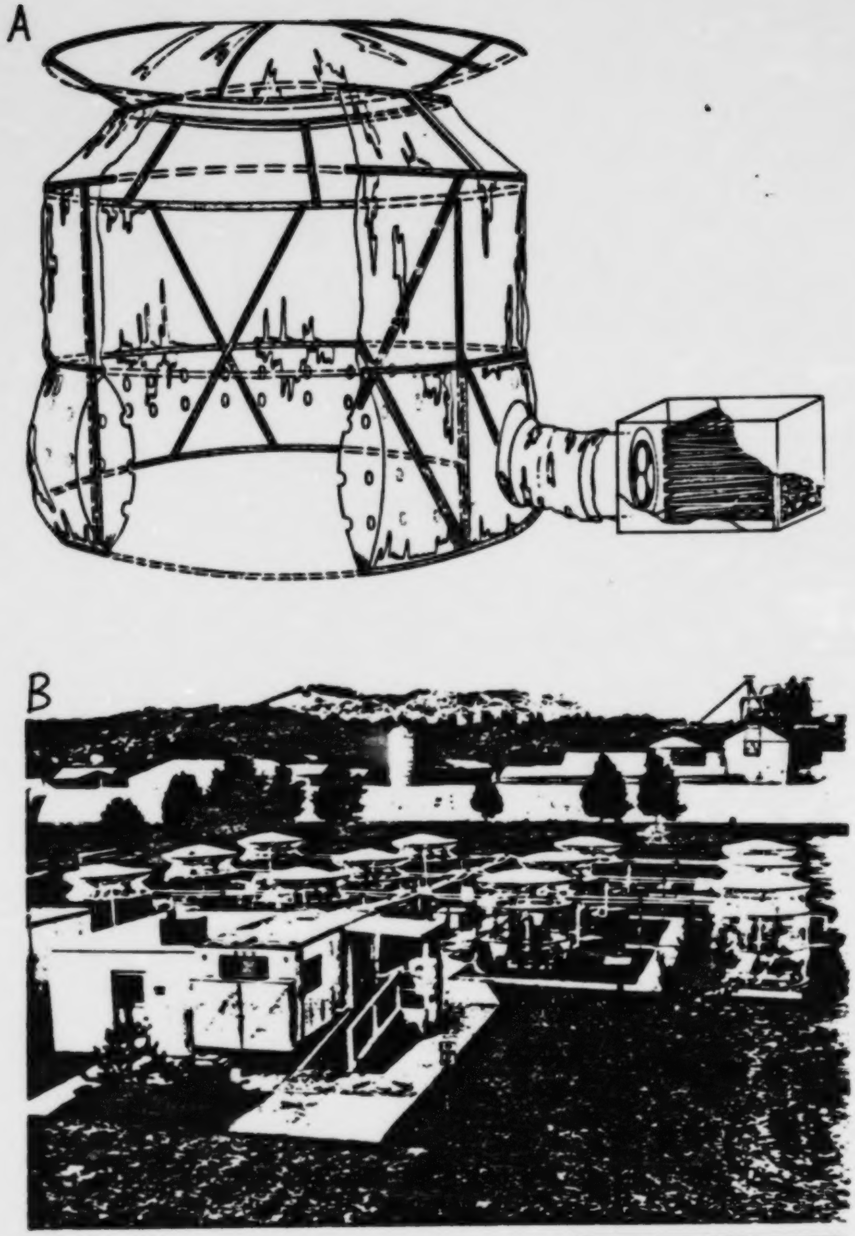

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Figure 9. Example of an open-top chamber. (A) An illustration showing the construction of a modified open-top chamber, and (B) an experimental location using a number of modified open-top chambers. The modifications include the addition of a frustrum to reduce the ingression of ambient air, a rain cap required for particular experimental studies, and netting over the open portion of the chamber to exclude insects.

blown into the chamber through a perforated air duct (plenum) around the chamber base. The air flows into the bottom of the plant canopy and then moves up and out the open top of the chamber. The movement of air out the open chamber top restricts the ingress of pollutants. Also, the open top allows rain to enter and causes only slight light attenuation and prevents significant temperature increases within the chamber. Comparable studies revealed only small differences in microclimatic parameters and the growth and yield of plants in chambers without air filtration and in adjacent plots without chambers (Heagle et al., 1979c, 1979e; Heck et al., 1982; Heggestad et al., 1980; Montes et al., 1982). The small difference in microclimatic conditions may have no significant effect on plant growth during the summer when light and temperature are generally not limiting. However, with the low temperatures and reduced solar radiation that occur during the winter in Great Britain (Greenwood et al., 1982), there is no reason for the assumption that the sensitivity of cereal plants grown in chambers over winter should be similar to that of plants growing in the field. Shinn et al. (1976) suggeted that open-top chambers had several disadvantages.

The chambers can be placed over plants growing in the soil or they can be filled with potted plants. In addition to the comparative studies with and without air filtration, the open-top chambers can be used in gaseous exposure studies in which measured amounts of particular pollutants are added.

In general, open-top chambers are reasonably well suited for establishing air pollution-induced yield losses, particularly in agricultural and horticultural plant species with a reasonable expenditure. Open-top chambers were selected for use in the NCLAN (National Crop Loss Assessment

Program) program (see Section 2.5.3.1), whose goal is to determine air pollution-induced yield reductions for agricultural crops in the United States and to study the dose-response relationships for O_3, SO_2, NO_2, and their mixtures. The NCLAN program employed these chambers because of the good results obtained in studies over several years.

3.4.2.2.2 Field Exposure Systems Without Chambers

The need to study air pollution effects on large plots and the goal of eliminating the potential chamber influence on the plant environment lead to the development of field exposure systems without chambers. Examples of these systems are the linear gradient system (Shinn et al., 1976), the zonal air pollution system (Lee and Lewis, 1978), and the computer-controlled system of Greenwood et al. (1982). Each system will be briefly described to show the progress in developing new methods. These systems vary in the amount of control that is used in applying the air pollutant to the plot.

The linear gradient system has been used both as an exclusion and as a fumigation system in the field (Shinn et al., 1977; Reich et al., 1982). This system utilizes a series of inflated polymer film tubes, under positive pressure, to distribute either carbon-filtered air or a mixture of fumigtant and filtered air over the plot. The inflated tubes are positioned between rows of plants with precalibrated holes oriented towards the plant canopy. The filtered air or fumigant gas mixture is emitted from the holes and permeates into and through the canopy. The linear gradient in gas concentration along the inflated tube is obtained by: i) a linear increase in gas discharged from the plenum (tubes); and ii) by increasing portal areas along its length combined with a constant exit velocity of the gas mixture. Because plants can be exposed to a large range of gas concentrations simultaneously, this method allows statistical regression analysis of the dose-response data. The original system was a rectangle 7.5 m long and 3 m wide encircled with clear fiberglass panels 0.6 m high. Technically, this is also a chamber as expressed in the title," A Linear-Gradient Chamber for Exposing Field Plants to Controlled Levels of Air Pollutants" of the publication by Shinn et al. (1977). The minimal influence of the small enclosure on the growth conditions of the plot and the use of the linear-gradient system without the enclosure (Reich et al., 1982) justifies the inclusion of this method under field exposure systems without chambers. As shown by experimental results, this system and the following two systems to be discussed, are strongly influenced by wind speed and direction.

The Zonal Air Pollution System (ZAPS) was designed to cause minimal disturbance to the biota, prey refuges, ground level obstructions and pathways, incident radiation, and microclimate. The original ZAPS consisted of a network of 2.54 cm diameter aluminum pipes suspended about 75 cm above 0.5 hectare plots of native grasslands (Lee and Lewis, 1978). Gas release ports (0.8 mm diameter) were positioned at 3-m intervals with more than 250 ports per 0.5 hectare plot and with no location more than 5.5 m from a port. The experimental design consisted of a series of plots each receiving a different SO_2 exposure. The control plot was arranged to minimize the drift of SO_2 from the test plots. Also, the control was selected to be as similar to the test plots as possible.

The ZAPS field exposure system relies on atmospheric diffusion to dilute a very high concentration of SO_2/air mixture released from the pipes. When the rate of release is constant, the resultant concentration depends largely on wind speed and can reach high levels at night when wind speeds are low. These diurnal concentration patterns follow atmospheric mixing with the minimum concentrations occurring during mid-day and the highest concentrations occurring at night when the air is still. However, this diurnal concentration pattern is different than that observed in rural England (Greenwood et al., 1982). Also, the pollutant distribution over the crop may be very uneven. When there is large variation, there may not be enough plants available for sequential harvests. To avoid the problem of high concentrations, the release rate can be reduced during conditions of poor dilution or when the wind is from a specified direction. The ZAPS system has also been adapted for use in determining the effects of SO_2 on crops grown under normal field conditions (Miller et al., 1980).

Greenwood et al. (1982) developed a computer-controlled system for exposing a normally-managed field crop (an area of about 400 m^2) to controlled concentrations of SO_2. The system allows plants to be successfully exposed to predetermined concentrations of SO_2 under essentially natural conditions. In principle, the system is also suitable for other gaseous air pollutants. The gas is released from pipes at a rate which can be varied by a microcomputer which also controls the monitoring of the SO_2 concentration. The SO_2 release rate depends on the measured concentration and wind speed. The computer control of the SO_2 release yields a much smaller variation in concentration than in the relatively uncontrolled ZAPS system. The simple, symmetrical design of the SO_2 release system enables large numbers of plants to be exposed as in a gradient system, allowing regular removal of plants for analysis without seriously modifying the crop environment.

3.4.2.3 Studies in Managed and Controlled Conditions

Both types of exposure systems will be discussed in a single section because of their similarities and to highlight their differences. Both types of exposure systems may be used in either greenhouses or controlled-environment chambers; the plants are placed in a closed area and subjected to a definite mixture of air and air pollutant. The plants may be exposed to the pollutants in separate units, i.e., several small greenhouses or controlled-environment chambers arranged close to each other or in subunits (chambers) located within either a greenhouse or controlled-environment chambers (Guderian, 1977). In the first case, the greenhouse or controlled-environment chamber serves directly as the exposure chamber; in the second case it provides only the "climatic conditions" and the exposures are conducted in specially designed chambers. The basic requirements of closed chambers (Heagle and Philbeck, 1978) in managed and controlled conditions are similar in principle:

- environment resembles ambient conditions;
- uniform environment throughout the chamber and among the chambers;
- transparent covering minimizing changes in light intensity and quality;
- non-reactive surfaces;
- capability or preparing, maintaining, and monitoring defined levels of known air pollutants;
- uniform pollutant concentrations throughout the chamber and among chambers.

In addition to these characteristics, the following ones are desirable: single-pass-continuous air flow system, negative pressure within the chamber, ease of moving plants in and out of the chamber, easy to build and clean, durable, and relatively inexpensive.

Naturally, these ideal requirements are only partially attained. In general, the extent that these goals are reached increases with the technology used, and the financial resources and inventiveness of the individual investigators. The exposure systems developed for use in closed chambers varied in complexity from relatively simple apparatus with only a limited capability of controlling the pollutant expousre and climatic conditions to increasingly sophisticated systems for control and regulation. It should be emphasized that these individual goals may be realized to varying degrees in various experimental designs in managed or controlled conditions. The key difference between the exposures in greenhouses and controlled environment rooms is the degree to which light, temperature, and relative humidity are regulated. Studies in greenhouses usually follow the natural fluctuating environmental conditions, light intensity, photoperiod, temperature, and relative humidity with some modification via the "greenhouse effect." For special experimental studies, there may be partial control of temperature and/or relative humidity. Plants may be exposed under artificial light but usually the artificial light is only supplementary. The advantages of experimental studies in greenhouses (with or without partial climate control), compared to controlled-environment rooms, reside in less deviation from the natural conditions and also in the larger number of plants and taller plants such as fruit or forest trees that can be exposed. The disadvantages are less control of environmental conditions and possibly pollutant exposure which may make it difficult to reproduce experimental results.

Reproducibility is the basic advantage of controlled-environment rooms. The capability of controlling pollutant exposure and climatic conditions to the levels desired provides the ideal conditions for investigating the influence of individual parameters on plant response to air pollutants. Controlled-environment studies are particularly well suited for determining the mode of action of individual pollutants, for studies of cause and effect, for hypothsis testing, and for determining dose-response relationships using acute short-term injurious concentrations. With long-term exposures, there is the persistent problem of extrapolating the experimental results to ambient conditions, particularly when light quality or intensity deviates substantially from natural conditions.

In the 80 years since Wislecenus (1901) conducted the first exposures in "ventilated smoke houses" with controlled air exchange, numerous and various exposure systems have been developed for use in the greenhouse and controlled-environment chambers. The details of construction and function of these systems are contained in the individual publications. An example of the newer developments is the Continuous Stirred Tank Reactor (CSTR) system (Rogers et al., 1977). In modified form, CSTR systems are recommended for use in greenhouses (Heck et al., 1978). Greenhouses may also be used as exposure systems for determining air pollution effects are contained in several publications (e.g., Berry, 1970; Guderian, 1977).

3.4.3 Summary Evaluation

At the beginning of this section, three basic requirements for studies of air pollution effects were postulated: i) they must be representative of typical conditions; ii) the cause-effect relationships must be assured, that is to say, the effect must be unequivocally related to a specific cause; and iii) finally the exposure and its effect must be quantified. These goals may not be met with a single exposure system because of the need to determine effects at various organizational levels of the ecosystem and the numerous factors that influence plant response. These were discussed in the subsections of Experimental Methods (3.4.2) and in the comparisons in Table 9. This generalization holds: with increasing deviations from natural conditions, it becomes increasingly difficult to establish "typical" results. Experiments using controlled or managed systems are particularly well suited for studies addressing the mode of action, to clarify etiological questions, and for hypothesis testing. In contrast, under natural conditions in congested areas, the determination of the phytotoxic components creates a problem that is not readily solved. Also, the evaluation of dose-response relationships and the spatial distribution and intensity of injury are difficult to determine because of problems in determining the emissions and exposure with sufficient accuracy. The advantages of studies in natural conditions are: no problems in extrapolating to natural conditions as well as the capability of determining the long-term effects on various components in the ecosystem.

In the area of exposure methods, the decisive progress in the last decade has been in the development of systems with and without chambers for studies that allow minimum deviation from natural conditions. Given their significant advantages as experimental systems in controlled and natural conditions they can be adapted for studies addressing a wide range of questions.

Table 9. Comparison of Experimental Methods Under Various Experimental Conditions

Characteristic Factors	Controlled	Managed	Semi-natural	Natural
Pollutant exposure.	The pollutant concentration and exposure duration are controlled as well as the frequency and sequence of exposure.	The pollutant concentration and exposure duration are controlled as well as the frequency and sequence of exposure, however, the concentration may be only partially controlled.	Exposure controlled or in some cases only partial control of pollutant concentration, duration, exposure frequency, and sequence.	Continuous variation in pollutant exposure.
Climatic factors.	Individual factors can be controlled with variable deviations from the natural climatic conditions.	Unless there is partial climate control, climatic conditions vary as in ambient except for the influence of the "greenhouse effect."	In open-top chambers, the conditions approach the natural; in exposure systems without chambers, there is even less deviation from the ambient conditions.	Natural conditions.
Plant culture and exposure.	Cultured in pots.	May be cultured in pots or soil.	Plants usually grown in soil but pot culture may be used.	Plants grown in soil.
Exposure susceptibility of the plants.	Depending on the climatic conditions, approximately normal to abnormal predisposition.	Approximately normal with more or less deviation from normal predisposition.	Approximately normal predisposition.	Normal predisposition.

(continued)

Table 9 (continued)

Characteristic Factors	Controlled	Managed	Semi-natural	Natural
Evaluation	Reproducible studies, particular characteristics: evaluation of the significance of individual factors on plant response, for studies of the mode of action on or in plants, for determining cause and effect and testing hypotheses, for short-term studies up to a few months, limited suitability for determining dose-response relationships at higher concentrations.	Limited multifactorial, in certain experiments limited reprocibility, particular uses: determination of the significance of particular individual factors for the study of the mode of action on o in plants and model plant communities, for cause-effects analysis, limited suitability for study of dose-response experiments possible over a period of a few years.	Limited multifactorial, limited reproduciblity of exposure studies, when used as pollutant exclusion systems, not reproducible; particular uses: determination of growth and yield losses, dose-response relationships, effects on plant communities, experiments possible overa period of several years.	Always multifactorial, experiments not reproducible, particular uses: determination of injurious effects on various components on ecosystems such as producer, consumers, and decomposers, determination of long-term effects on forest plants and plant communities.

CHAPTER 4
FACTORS INFLUENCING PLANT RESPONSES

The occurrence and magnitude of vegetation effects are dependent on the concentration, frequency and duration of exposure, time between exposures, the magnitude of the concentration changes, diurnal timing of exposures, their sequence and pattern, and ozone flux into the plant as it is influenced by canopy characteristics and the leaf boundary layer (Jacobson, 1982). Most ozone response studies have considered only the concentration and duration of exposures while the other parameters that also influence pollutant response have received only cursory study.

Plant reactions to a given air pollutant depend on the exposure parameters which may be modified by internal and external growth factors. The previous chapters described various photochemical oxidant effects and methods to evaluate them. This chapter discusses factors that influence plant response and provides information to help understand and evaluate the dose-response relationships discussed in Chapter 6.

4.1 Concentration and Duration of Expcsure

Knowledge of the quantitative relationship between the ambient exposure and effect is important for air pollution studies: (1) it provides information important to understanding pollutant-induced effects, and (2) it provides the basis for protective measures based on air quality principles. Recognition of these needs led to the development of dose-response relationships. The magnitude and expense of these studies result from the difficulty of developing reliable dose-response relationships that can be used as a basis for general risk predictions to vegetation.

The relationship between ambient exposure and effect can be characterized with sigmoid curves (Figure 10). Below a specific dose (D_1), the reactions of even the most susceptible plants do not deviate significantly

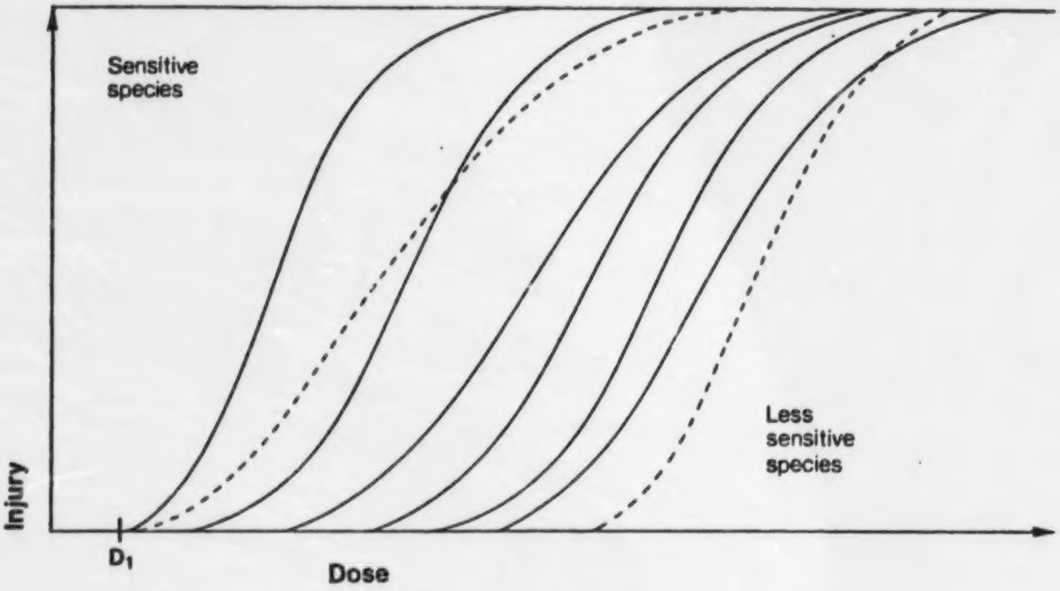

Figure 10. Schematic representation of dose-response relationships for differentially susceptible plant species. Dose is the product of the ambient concentration multiplied by exposure duration.

from the normal variation of unexposed controls. Above the corresponding response threshold, responses can be observed which may be relevant for practical environmental protection. The threshold doses are different for different measures (i.e., injury, yield, quality) of response. With increasing dose, the response rapidly increases (monotonically) to a higher response level, then the curve flattens and approaches, asymptotically the maximum response level, e.g., 100% leaf necrosis. Differential resistance of individual plant species is expressed in the correspondingly higher doses required to cause injury. The variable steepness of the response curves for the individual plant species results from changes in the dependency of differential species resistance relationships on the dose levels (compare 4.3.2).

For ozone, PAN and other phytotoxic gases, dose alone is not a sufficient parameter to determine responses or describe effects. For a given pollutant dose, plant responses vary with concentration, exposure duration, frequency, or exposure sequence.

Injury from photochemical oxidants, PAN, and ozone increases exponentially with exposure. Heck et al. (1966) clearly showed this relationship between ozone concentration, exposure duration, and injury to bean foliage using a three dimensional model (Figure 11). The three-dimensional figure illustrates the resultant foliar injury from various combinations of ozone concentration and exposure duration. The shape of the surface depicts the variable interaction between concentration and duration in producing injury. For example, in bean plants injury occurred above a specific concentration or duration of exposure. The steepness of the concentration and time planes of the response surface illustrates how differential injury can result from only small changes in pollutant dose. In addition, it

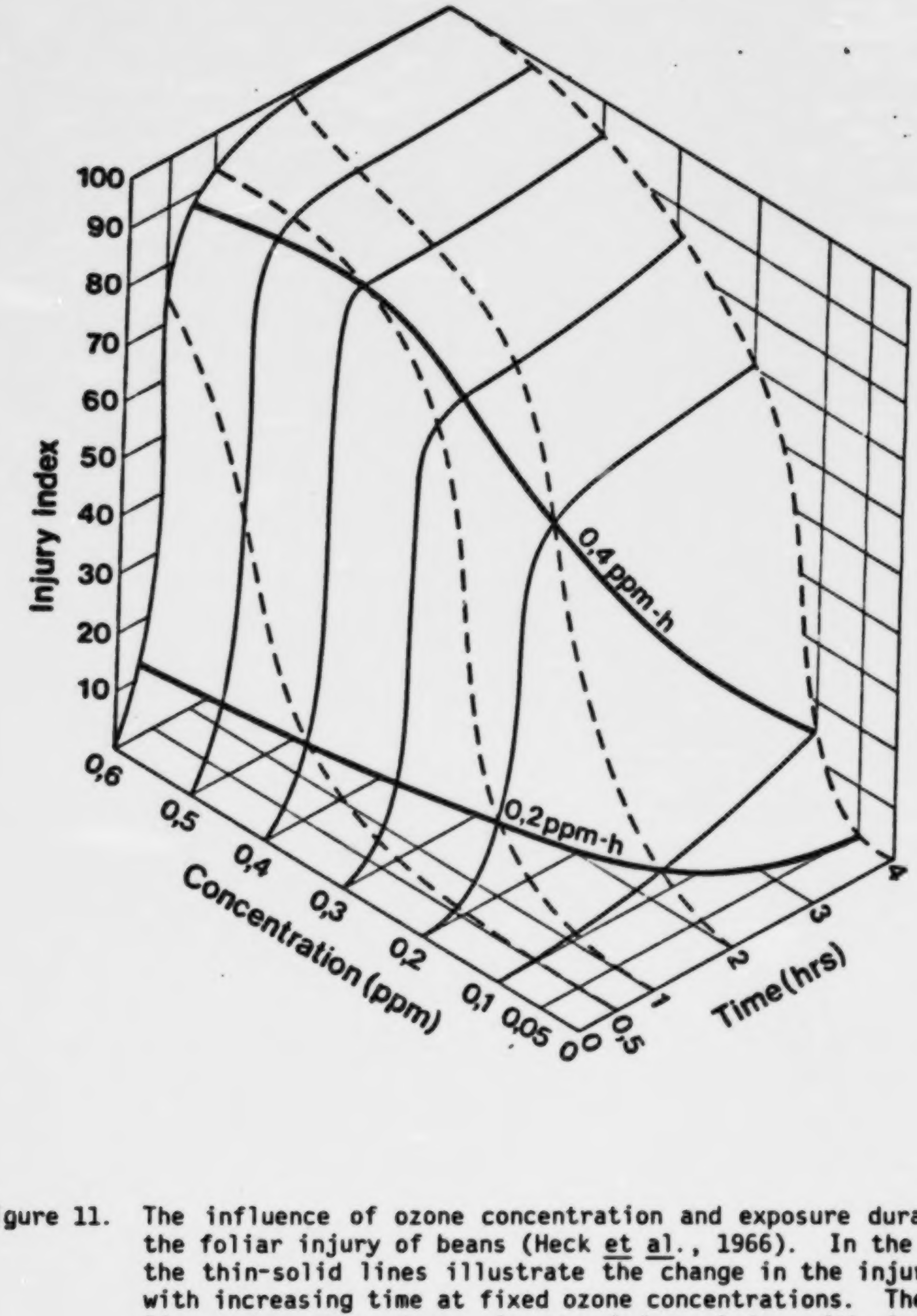

Figure 11. The influence of ozone concentration and exposure duration on the foliar injury of beans (Heck et al., 1966). In the figure, the thin-solid lines illustrate the change in the injury index with increasing time at fixed ozone concentrations. The dashed lines show the change in the injury index with increasing concentration at fix time intervals; the two wide-solid lines show the change in the injury index at two constant ozone doses.

follows that the same dose in a short time will cause a stronger response than when the dose is distributed over a longer time period. The relationship between pollutant dose and effect usually does not follow the case where a specific dose always induces the same magnitude of response. The extent of foliar injury increases progressively with increasing concentration when equal products of concentration (c) and exposure duration (t) are used as was previously observed for sulfur dioxide (Van Haut, 1961). Plant growth is also influenced more by concentration than exposure duration when similar products of c and t are used (Guderian, 1966). Peak concentrations pose a particular risk to vegetation, especially when they rapidly follow one another.

The following examples confirm that for ozone, concentration is the important exposure parameter controlling plant response. Following a 1-h exposure at 0.50 ppm ozone (dose = 0.50 ppm*h), the secondary needles of 3-year-old Virginia pine seedlings displayed 50% necrosis while after an 8 h exposure at 0.10 ppm (dose = 0.80 ppm*h) only 10% necrosis resulted (Davis and Wood, 1973b). During chronic exposures, the injury increased with increasing concentration. For example, the net photosynthetic rate of ponderosa pine seedlings was reduced 25% following exposure to 0.15 ppm ozone for 9 h/day for 60 days, while doubling the concentration (0.30 ppm) and reducing the exposure duration to 30 days reduced net photosynthesis 67%. In both studies the product of concentration and time (dose) was 81 ppm*h (Miller _et_ _al_., 1969). Additional examples of the greater importance of concentration compared to exposure duration have been given by numerous authors (e.g., Ross _et_ _al_., 1976; Reinert and Nelson, 1979; Henderson and Reinert, 1979; Shertz _et_ _al_., 1980b).

The importance of concentration does not hold for all combinations of ozone concentration and time. In one study using very low ozone concentrations producing the same dose (1.2 ppm*h), a 24-h exposure at 0.05 ppm reduced the growth of bean foliage more than a 12 h exposure at twice the concentration (Evans, 1973). Isolated instances of growth stimulation at very low ozone (Barnes, 1972a; Bennett et al., 1974; Runeckles and Resh, 1975b; Lumis and Ormrod, 1978; Leone and Brennan, 1975) and PAN (Temple, 1982) concentrations have been reported as has been observed with other pollutants (Guderian, 1977).

The particular importance of concentration for inducing injury responses was considered in efforts to formulate mathematical relationships between the pollutant exposure and effect. O'Gara (1922) derived the following equation from acute exposures using sulfur dioxide:

$$c = a + b/t$$

where:

c = concentration in ppm

a = threshold concentration, that for a given exposure duration will not cause any injury

b = constant, that reflects internal and environmental factors that influence plant sensitivity

t = exposure duration in h

The relationship proposed by O'Gara (Figure 19) agrees well with results obtained from short term ozone exposures. The functions (Guderian et al., 1960; Zahn, 1963) established to determine the concentration-dependent risks of chronic SO_2 exposures will not be considered further because the assumptions for their use with chronic ozone and PAN exposures are lacking.

Several methods have been proposed to describe chronic or seasonal ozone exposures for vegetation effect studies in the field. Heagle et al. (1979a, 1979b, 1979e) used the 7-h (0930 to 1630)/day seasonal mean concentration for injury, growth, and yield studies in the field. However, this method treats low-level long-term exposures the same as high concentration, short-term exposures that may produce a similar dose and it is inconsistent with the observed dose-response relationships described above. A seasonal ozone dose has been calculated by summing the hourly ozone concentrations above a threshold concentration (Oshima, 1974b; Oshima et al., 1976). However, this method requires the calculations to be made from actual hourly data. Recently, Lefohn and Benedict (1982) proposed an exposure index that also determines the ozone exposure above a threshold but which can be calculated from either actual data or frequency distributions. The approaches of both Oshima and Lefohn and Benedict include the concentration, duration, and frequency of exposure in the exposure index in constrast to the 7-h average of Heagle et al.

The establishment of a mathematical relationship between pollutant exposure and effect is made more difficult because phytotoxic concentrations of photochemical oxidants occur only under specific meterological conditions and during specific hours of the light period. Exposure periods from anthropogenic-induced ozone are interspersed with pollution-free periods when only the natural background concentration occurs. From investigations with sulfur dioxide it is known that the pollutant-free periods serve as a recovery time if the given concentration and the exposure period are not too long and the pollutant-free period exceeds a minimum time (Zahn, 1963; Guderian, 1970). In any case, the results of from discontinuous exposures can be different from continuous. ones of the same dose.

A continuous ozone exposure from 1-h produced more foliar injury on bean and tobacco plants than two 0.5-h exposures occurring within 1 to 3 h (Heck and Dunning, 1967). Tobacco plants exposed to ambient oxidant for 7 days in non-filtered chambers developed more than twice as much injury during the period than the summed injury on individual plants exposed to ambient oxidant for only 1 day each (Heagle and Heck, 1974). In contrast, the reduction in hypocotyl growth of radish plants exposed to ozone at 7-day intervals was the sum of the individual reductions during the corresponding development stages (Tingey et al., 1973a). In studies with sweet corn and tomatoes, Oshima (1974b) found that the frequency of ozone exposure appeared to be as critical a factor as total dosage in long-term exposures. A greater number of relatively short-term exposures had a larger effect than fewer exposures of greater duration. Studies with kidney beans showed that exposures from constant concentrations of ozone caused the same pattern of response as variable concentrations of equivalent dose (Musselman et al., 1983). However, the variable-concentration exposures reduced plant growth to a greater extent.

These limited results do not support their use in the development of models of dose-response relationships. However, they underscore the importance of outdoor and field studies for the development of air quality criteria.

The above presentation provide evidence that high concentration-short term exposures may produce different relationships between exposure parameters -- concentration, duration, and frequency of exposure -- than chronic continuous low-level or intermittent exposures. In practice, vegetation injury represents both acute and chronic concentrations that display large spatial and temporal changes (EPA, 1978a). There is general agreement (Heggestad and Heck, 1971; Linzon et al., 1975; Heck and Brandt, 1977) that necessary prerequisites needed to model the risks from chronic and intermittent exposures are lacking. The evaluation of short term effects of acute injurious concentrations has allowed the development of concepts as aids for the evaluation and incorporation of the extensive experimental results into general concepts (see Chapter 6.2).

4.2 Significance of External Growth Factors on Plant Sensitivity

External growth factors include edaphic and climatic conditions. These factors influence gas phase conductance, pollutant uptake and its reactions within the plant: directly during and following an exposure and indirectly before exposure through their influences on the physiology and morphology of the plant. The stomata are the primary portal of pollutant uptake into the plant (see 2.1) and a significant factor controlling gas uptake. Therefore, any external factor that influences stomatal opening would also influence pollutant uptake.

In the field, these external factors can interact and modify plant responses. In some cases, the relationship between exposure and response is altered without knowing which of the environmental factors caused the change. For this reason, controlled conditions are used to study the influence of external factors on plant response.

4.2.1 Climatic Factors

The climatic conditions before, during, and following exposure influence the type and intensity of the plant response to a given pollutant exposure. Certain climatic conditions preceding an exposure increase the susceptibility, while others reduce it. The major significance of climatic conditions during exposure is explained through their influence on pollutant absorption and its reactions within the plant. Climatic conditions following exposure are generally of lesser importance. From the complex of possible conditions, the parameters of light, temperature, and relative humidity will be considered.

4.2.1.1 Light

The presentation considers the influences of the following light parameters: photoperiod, intensity, and quality on pollutant uptake and reactions.

4.2.1.1.1 Photoperiod

Photoperiod is the length of the light period in an alternating light-dark cycle. Pollutant absorption and injury are frequently greater in the light than in the dark, corresponding to the light-induced increase in stomatal opening. The stomata of most plants are closed in the dark; therefore exposures during this period are generally less injurious. For example, a 3-h dark treatment just prior to exposure in dim light was sufficient to decrease the stomatal aperture and to reduce ozone injury to tomato foliage (Adedipe _et_ _al_., 1973b). However, pollutant uptake can occur in the dark. Sulfur accumulation in plants exposed to SO_2 in the dark was one-third the accumulation in the light (Guderian, 1970).

The influence of light on plant responses to photochemical oxidants goes beyond a simple influence on stomatal opening during or just prior to exposure. For the development of PAN injury in pinto beans, light was required before, during, and following exposure. The injury decreased with the duration of the light period before exposure (Dugger _et_ _al_., 1963b) and also the duration following (Taylor, 1969). The injury was maximal when there was at least 3 h of light following exposure, given light both before and during exposure. A dark period as brief as 15 min preceding a 30-min PAN exposure in the light reduced injury. Given light before and during exposure, the symptom expression depended on the light or dark periods following exposure: 100% injury with 3 h or more of light, 0% injury with 2 h or more of darkness; shorter light or dark phases produced proportional amounts of injury at comparable PAN concentrations (Taylor, 1969). The mode of action is unknown.

In contrast, for ozone there is not absolute light requirement injury to develop. Taylor _et_ _al_. (1961) found that light before, during, or following exposure was without influence, while a 24-h dark period before exposure reduced ozone sensitivity in cotton plants (Ting and Dugger, 1968). A 24-h light period before exposure reduced the sensitivity of young Virginia pine plants (Davis, 1970).

In addition to the direct effects of light on pollutant absorption and response, it also has a significant influence on the physiological condition of the plant. Therefore, light conditions including photoperiod during plant culture control the plant's predisposition to air pollutants. For example, annual bluegrass (_Poa_ _annua_) was more sensitive when cultured under an 8-h photoperiod than under a 16-h one (Juhren _et_ _al_., 1957). Cultivated plants were more sensitive when grown at an 8 h than either a

12- or 16-h light period (MacDowall, 1965a; Heck and Dunning, 1967). The relatively high resistance of plants grown on long days was diminished by only a 3-day conditioning period at short days prior to exposure.

4.2.1.1.2 Light Quality

Possibly the oxidant-sensitivity of plants is altered by a compound that under the influence of light is converted from an inactive to an active form (or reversed). In searching for such a substance, Dugger et al. (1963b) determined that the amount of ozone injury depended on the wavelength of light. The most injury occurred between the wavelengths of 420 and 480 nm. In this wavelength range, the principal chromogens are carotenoids. Carotenoids react readily with atomic oxygen that is liberated by the reaction of PAN with bases (Steer et al., 1969). It is not clear if these facts are actually related.

Sulfhydryl compounds are among the preferential reaction sites for photochemical oxidants and, in conjunction with other compounds, influence the sensitivity of the leaf. Their synthesis was increased with increasing light intensity; the two light reactions (I and II) of photosynthesis had a differential effect on synthesis (Dugger and Ting, 1968). Irradiation with 660 nm light activated photosystem II, whereby a larger amount of sulfhydryl compounds were produced than by the activation of photosystem I at 700 nm (Dugger and Ting, 1968). The situation is confused if one considers that the phytochrome system absorbs in similar wavelengths with changes in its activity: illumination with 660 nm light converts P_r to P_{fr}; the back reaction follows from either dark or irradiation with 730 nm light. According to Butler et al. (1964), P_{fr} but not P_r reacted with sulfhydryl reagents.

4.2.1.1.3 Light Intensity

Besides the duration of light and the wavelength, light intensity before, during, and following pollutant exposure influenced plant reactions. In controlled pollutant exposures, increasing light intensity during exposure increased plant injury. With pinto beans, a positive correlation was established between the amount of ozone injury and light intensity up to 32.3 klux (Juhren et al., 1957; Heck et al., 1965). Short-term ozone exposures induced more injury in pinto bean at 43 klux than at 21.5 klux (Dunning and Heck, 1973). In similar experiments, pinto beans grown at 43 klux had less injury than those grown at 21.5 and 10.7 klux, while Bel W_3 tobacco reacted oppositely (Dunning and Heck, 1977). Following a short-term ozone exposure, tobacco and pinto beans were more injured when grown at 21.5 klux than 32.3 klux (Heck and Dunning, 1967). Plants exposed to injurious concentrations of SO_2 and O_3 in the light (16 klux) were severely injured; injury intensity decreased with decreasing light intensity and only minor injury resulted from exposures in the dark (Yamazoe and Mayumi, 1977). Light or dark for 24-h before or following exposure did not influence the amount of injury.

Although these observations are not without contradictions and are based on only three plant species, a generalization can be made; low light intensity during plant growth increased the sensitivity to photochemical oxidants, while increasing light intensity during exposure increased injury. With longer exposures in ambient conditions, both light responses are superimposed so, for example, a high light intensity during pollutant exposure will momentarily increase the injury, while concurrently the plant sensitivity to a later exposure may be reduced.

In the dark, stomata are generally closed -- except for plants of the Solanaceae family -- and during photochemical oxidant exposure, plant injury is reduced; at approximately 1000 lux with stomatal opening injury is observed (Heck et al., 1965). High light intensities during exposures in the field are less likely to cause maximum foliar injury than under laboratory conditions because the plants in the field experience intense solar irradiation, temperature extremes, and possibly water stress which leads to partial stomatal closure.

4.2.1.2 Temperature

The temperature during plant growth and exposure has a significant influence on plant sensitivity to photochemical oxidants. Studies with various plant species clearly showed that plant sensitivity to ozone increased with growth temperature over the range of 3 to 30 C (Dunning et al., 1974; Shinohara et al., 1973; Dunning and Heck, 1977; Davis, 1970; Davis and Wood, 1973a; Wilhour, 1970b). In radishes, foliar injury increased with increasing growth temperature, but the ozone effect on root growth was similar over a range of growth temperatures (Tingey et al., 1973a). Sensitivity of various vegetable plants to ozonated hexene and other alkenes increased with increasing growth temperature (Hull and Went, 1952; Kendrick et al., 1953; Middleton, 1956). The influence of temperature was expressed to a greater extent the longer the plants were maintained at a particular growth temperature before pollutant exposure (Hull and Went, 1952; Kendrick et al., 1953; Middleton, 1956). Plant sensitivity to ozone decreased when the growth temperature exceeded 30 C (MacDowall, 1965a).

With annual bluegrass (Poa annua), Juhren et al. (1957) showed that the temperature response during plant growth depended on the respective diurnal temperature cycles and the particular developmental phase of the leaves. During the development of the cotyledonary leaves, the sensitivity was greatest at high temperatures (30 C day; 24 C night); however, it was significantly reduced by the time that the third or fourth leaves developed. Under cool conditions (20 C day; 14 C night), the sensitivity in the 2-leaf stage was low, gradually increased with age until about 6 weeks and then decreased. In cold conditions, the plant remained uninjured until flowering started. Four-week-old plants were most sensitive when grown at a temperature range of 26/20 or 23/17 C, while plants in a moderately cooler (20/14 C) condition were somewhat less sensitive; the response of plants in a hotter environment (30/24 C) was reduced markedly. Plants grown in the mid-temperature range (26/20 C) lost their sensitivity after only 3 days of growth at a higher temperature (30/24 C).

MacDowall (1965a) also observed that the ozone injury level was greater on plants grown at moderate temperatures than at higher ones. High night and low day temperatures also increased plant sensitivity (MacDowall, 1965b).

For most plants studied, foliar sensitivity increased with increasing growth temperature up to approximately 30 C; at higher temperatures this response was reversed. The magnitude of the temperature difference between day and night conditions may also influence the reponse; however, there have been too few studies to draw final conclusions. Also, the extent of time that the plant was preconditioning at a specific temperature regime influenced the amount of foliar injury (Middleton, 1956).

The relationships among growth temperature, ozone dose, and their influences on the foliar responses of pinto bean and soybean (Dunning et al., 1974) have been shown diagrammatically (Figure 12). While foliar injury levels for soybean increased considerably at higher growth temperature, pinto beans showed both increased and decreased sensitivity depending on the ozone dose. Considering exposure temperature, pinto bean displayed significant differences in foliar injury depending on the ozone dose, while foliar injury on soybean was similar at both exposure temperatures (Figure 13).

Later studies (Dunning and Heck, 1977) showed that 1-h exposures over the temperature range 16-27 C had no significant influence on the extent of injury to pinto bean or tobacco, but at 32 C injury on tobacco and pinto bean was significantly reduced and increased, respectively, compared to the lower temperatures. Shinohara et al. (1973) also found less ozone injury on tobacco exposed during high temperatures.

Under field conditions, ozone caused little or no foliar injury to corn when the ambient temperature was less than 32 C. Given similar conditions except with temperatures greater than 32 C, significant injury occurred (Cameron and Taylor, 1973). It is difficult to differentiate the influence of temperature and light intensity under field conditions (Juhren et al., 1957) where they interact with relative humidity and soil water content. Even though the individual factors can differentially influence plant sensitivity, they can give a very different picture under field conditions (see 4.2.3.2).

Through corresponding biochemical, physiological, and anatomical features, plants have adapted to various climatic conditions which at the same time can influence plant sensitivity to photochemical oxidants.

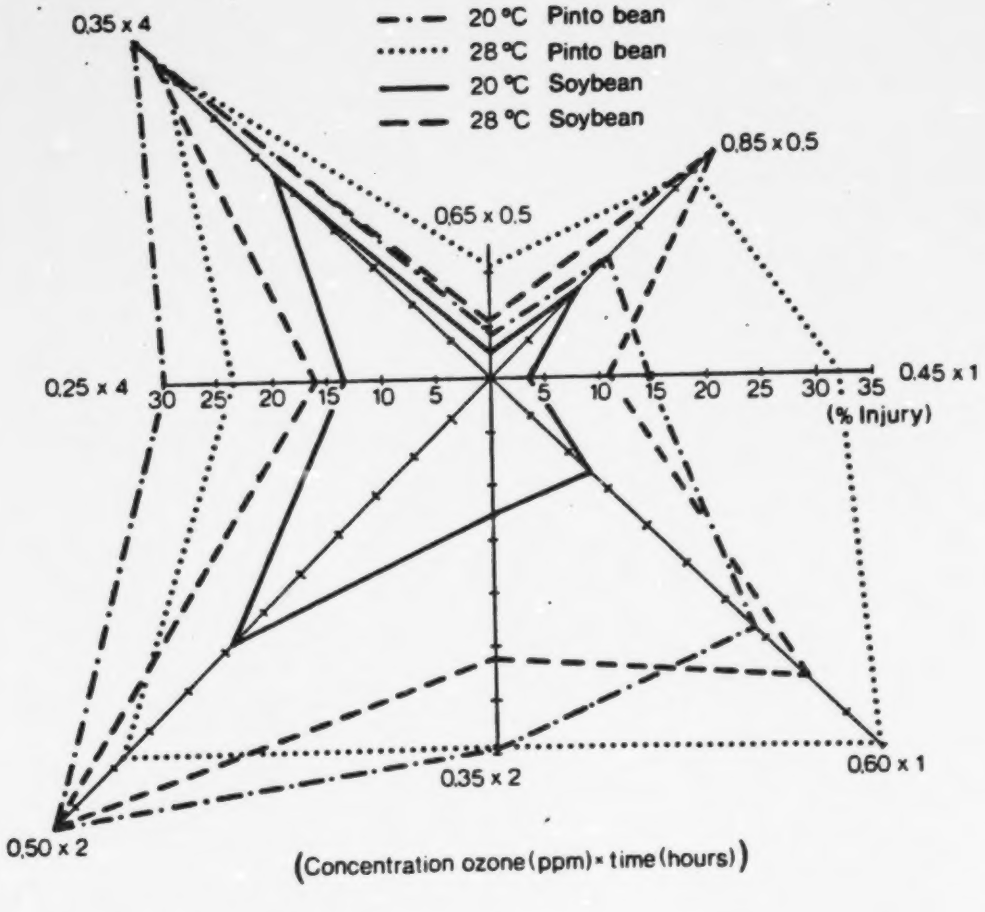

Figure 12. The interactions of growth temperatures (20 and 28 C), ozone concentrations, and exposure durations on the amount of foliar injury for pinto beans and soybeans (Dunning *et al*., 1974). Increasing exposure durations are shown in a clockwise manner around the figure; within each exposure duration, ozone concentrations increase clockwise.

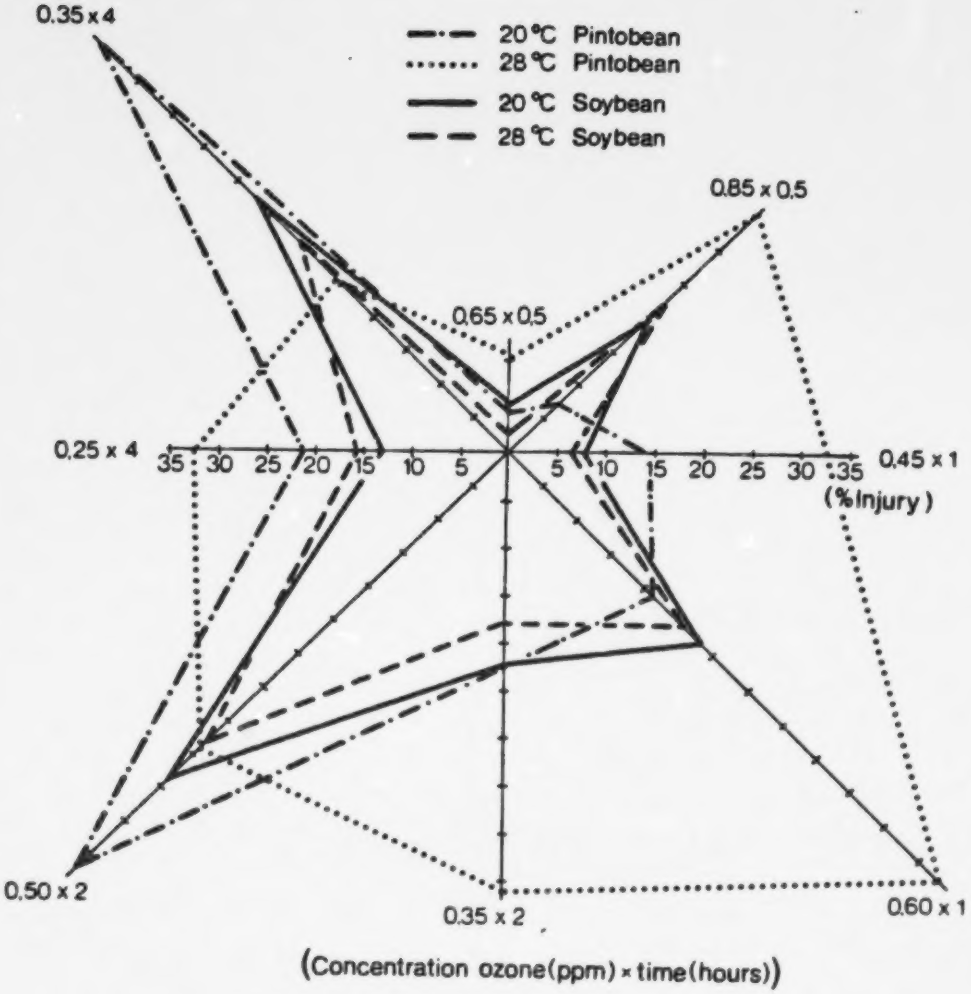

Figure 13. The interactions of exposure temperature (20 and 28 C), ozone concentrations, and exposure durations on the amount of foliar injury for pinto beans and soybeans (Dunning et al., 1974). Increasing exposure durations are shown in a clockwise manner around the figure; within each exposure duration, ozone concentrations increase clockwise.

During the exposures of a large number of turfgrass species and cultivars to ozone and PAN, Youngner and Nudge (1980) observed that the cool-season types were generally more sensitive than the warm-season types.

Although carbohydrate contents have been implicated in differential plant exposures (see Sections 4.3.1.2 and 4.3.2.1), they apparently do not account for the temperature-dependent changes in sensitivity. Dugger and Ting (1970b) concluded that sugar was not the sole factor controlling injury. Dunning et al. (1974) found no relation between the foliar carbohydrate content and the differential foliar injury response of soybean and pinto bean as it was influenced by growth and exposure temperatures. Adedipe and Ormrod (1974) found no consistent correlation between total soluble carbohydrate and ozone sensitivity as determined by growth reductions.

4.2.1.3 Relative Humidity

Relative humidity influences the leaf turgor and thereby controls stomatal opening and gas exchange. Pollutant uptake and plant injury increase with increasing relative humidity. In addition to the short-term effects of relative humidity on pollutant uptake, the long-term effects induce anatomical and morphological changes in leaves which may also effect pollutant uptake.

Using young Virginia pines, Davis (1970) established a correlation between the relative humdity during plant growth and the ozone-induced needle necrosis. Similar results were obtained with American ash (Wilhour, 1970b). With pinto bean, the injury intensity following short-term acute ozone exposures increased with the relative humidity during growth (Dunning and Heck, 1973, 1977), when the plants were grown at a light intensity of 21.5 klux, but not at 43 klux (Dunning and Heck, 1973).

During plant growth, relative humidity can also influence anatomical characteristics of the leaf. According to Rentschler (1973), plants grown at a low relative humidity developed thicker wax layers than those grown at a high relative humidity. The wax crystals that partially overlay the stomata were larger, more branched, and entwined, thereby reducing transpiration and also pollutant uptake through the stomata and cuticle. Plants grown at a low humidity also developed smaller stomata.

Otto and Daines (1969) and Rich and Turner (1972) showed that stomatal opening increased with relative humidity. Subsequent studies showed that foliar ozone uptake also increased with relative humidity (McLaughlin and Taylor, 1981). The extent of foliar ozone injury was correlated with relative humidity in American ash (Fraxinus americana) (Wilhour, 1970a, b), pinto bean and tobacco Bel W_3 (Otto and Daines, 1969; Dunning and Heck, 1973, 1977). With ozone exposures of tobacco, Menser (1963) established an increase in injury with increasing relative humidity. This principle has been shown by others (Hull and Went, 1952; Thomas and Hendricks, 1956; Leone and Brennan, 1969a). The relative humidity following exposures does not apparently influence foliar injury (Otto and Daines, 1969).

A water film on the leaf surface may elevate the relative humidity increasing the phytotoxicity of photochemical oxidants, however, the results are contradictory. Rain (MacDowall et al., 1963) or dew (Costonis and Sinclair, 1969a; Leone and Brennan, 1969a, 1969b) increased ozone injury on various plant species; however, MacDowall (1966) found no effect of dew on the ozone sensitivity of tobacco.

The discussed relationship between injury and relative humidity is important not only in the laboratory and greenhouse but also under field conditions. Under the generally more humid conditions in the eastern USA, ozone concentrations of 0.14 to 0.22 ppm as daily means may cause extensive plant injury, while ozone concentrations of 0.2 to 0.4 ppm may produce only limited injury in California where low humidity conditions can persist over extended periods (Heggestad et al., 1964; Heck et al., 1977b; EPA, 1978a).

Increasing relative humidity does not appear to have a practical influence on PAN effects. Taylor (1969) hypothesized that PAN would not occur in phytotoxic concentrations at elevated relative humidities because PAN is unstable at high humidity.

4.2.2 Soil and Nutrition

4.2.2.1 Soil Water Content

Soil water content, especially soil water deficiency, can have both short- and long-term effects on pollutant uptake. Short-term water stress impairs plant hydration, decreasing stomatal aperture and reducing pollutant uptake. Long-term water stress during plant growth causes physiological and morphological alterations reducing gas exchange and thereby pollutant uptake.

Fully turgid plants exposed to ozonated hexene were more severely injured than plants with a deficient water supply (Hull and Went, 1952; Koritz and Went, 1953). Water-stressed tomato plants lost only a small amount of chlorophyll when exposed to ozone compared to well-watered plants (Khatamian et al., 1973; Adedipe et al., 1973b). Similar results were found for bean and barley exposed to ozone and SO_2 (Markowski and Grzesiak, 1974). Pollutant uptake was reduced, as shown by the decreased sulfate enrichment in the water-stressed plants. The stomata of tobacco under water stress were generally closed, while the stomata of well watered plants were open even during ozone exposures (Rich and Turner, 1972). Water stress-induced protection from ozone injury can be obtained within 1 to a few days, depending on the severity of the water stress (G. S. Taylor et al., 1960; Tingey et al., 1982). The differential ozone response between two corn cultivars was associated with a greater sensitivity of one cultivar to water stress which induced stomatal closure reducing gas exchange (Harris and Heath, 1981).

The influence of water stress on plant sensitivity to photochemical oxidants is important in agricultural practice. G. S. Taylor et al. (1960) observed that field-grown tobacco plants, during drought periods, were protected by some means from photochemical oxidants. Foliar injury to tobacco in Ontario, Canada (Walker and Vickery, 1961), and Florida, USA (Dean and Davis, 1967), increased proportionally to the amount of irrigation water applied. In particular areas of the USA where tobacco is endangered by ozone, the tobacco farmers are informed over the radio of predicted periods of high photochemical oxidants and advised to restrict their irrigation as much as possible (Dean and Davis, 1972). Following a period of photochemical smog in California, well-watered grain plants exhibited extensive ozone and PAN injury, while plants grown in fields that had not been irrigated were uninjured (Taylor, 1974b). Obviously, water stress cannot be used as an avoidance mechanism for photochemical oxidant injury over the long term because water stress can significantly reduce plant productivity.

Tobacco plants that were grown under water-stressed conditions and then watered to field capacity a few hours before ozone exposure exhibited less injury than plants that were well watered during the total growth period (MacDowall, 1965a). Studies with water-stressed bean and tobacco plants showed that they became as sensitive to ozone as well-watered plants within a few days after the water stress was removed (G. S. Taylor et al., 1960; Tingey et al., 1982).

4.2.2.2 Elevated Salt Concentrations in the Soil Solution

Oertli (1959) grew sunflowers in sand culture using nutrient solutions of different osmotic potentials and salt contents to test their influence on plant response to photochemical smog. A high salt concentration in the solution produced a "physiological drought," reducing water uptake by the roots. Therefore, a negative correlation was found between the salt concentration in the nutrient solution and photochemical smog-induced foliar injury. High salt concentrations not only caused a physiological drought, but the elevated salt contents in the plant tissue may injure cellular metabolism and thereby alter plant response to photochemical oxidants.

Increased salt in the soil decreases the osmotic potential of the soil solution, restricting water uptake by the plants. With time this effect can, in part, be compensated for as a result of the increased passive uptake of salt which decreases the osmotic potential of the cell sap. In addition, the increased salt content of the tissue disrupts the ionic equilibrium in the cytoplasm producing changes in membrane permeability and alterations in cellular metabolism (Levitt, 1980).

Regardless of the cause, if the plant growth medium contains elevated salt concentratins the plants are less susceptible to photochemical oxidant injury. Chronic exposure to elevated soil salts coupled with increased evapotranspiration reduces plant hydration causing a partial stomatal closure (Levitt, 1980). Studies with beet (Beta vulgaris), alfalfa, and pinto bean found that plant growth was decreased as the salt concentration in the solution was increased to an osmotic potential of -84 kPa by alterations in metabolism and gas exchange (Ogata and Maas, 1973; Maas _et al_., 1973; Hoffman _et al_., 1973, 1975). Following an ozone exposure (0.10 to 0.35 ppm for a few h/day for 2 to 9 weeks), plant growth reductions were correlated with increasing ozone concentrations for the "salt free" plants but with increasing salt concentrations the magitude of the ozone effect was decreased. A similar antagonistic response was found with studies on young red maple (Acer rubrum) trees. The addition of 4000 ppm NaCl reduces growth more than 2000 ppm; the growth of plants at the high salt level was scarcely impacted by 0.25 ppm ozone (Dochinger and Townsend, 1979). In many areas, salt is used on roads as a de-icer and it may influence vegetation along the edge of highways raising the issue of possible interactions between salt and photochemical oxidants.

4.2.2.3 Plant Nutrients

Numerous elements are essential for plant growth; they are separated in two groups: macronutrients (nitrogen, potassium, calcium, magnesium, phosphorus, and sulfur) and micronutrients (chlorine, boron, iron, manganese, zinc, copper, molybdenum, and cobalt for nitrogen-fixing legumes). Nutrient deficiencies well as excesses can induce disease symptoms on the plants. In any case, the physiological condition of a plant is controlled by the corresponding nutrient supply. Because the physiological condition of the plant influences its susceptibility to photochemical oxidants, the plant nutrient status can significantly influence the plant response to a given ozone dose. However, this influence is neither qualitatively nor quantitatively reproducible because of "the number of experimental investigations is still quite small and presents an incomplete and controversial picture" (Guderian, 1977). General conclusions are not possible because of contradictory results. These discrepancies occur, in part, because of dissimilar experiental conditions and the use of various plant species at different developmental stages. The result is that it is not possible to given a general fertilization recommendation that will increase plant resistance to photochemical oxidants.

The effect of nitrogen nutrition has been studied by several groups. White Gold tobacco plants grown at an excess or deficiency of nitrogen were more severely injured than plants which received the optimal or slightly suboptimal levels (MacDowall, 1965a). The mechanism is not clear even though a correlation between stomatal opening and nitrogen nutrition was found. Leone _et_ _al_. (1966) reported different results for tobacco; injury was most severe on plants which received the optimal nitrogen level and less for plants that received either an excess or deficiency; they also observed that the plants grown on the optimal nitrogen level had the lowest carbohydrate contents. Low carbohydrate concentrations have been correlated with reduced plant susceptibility in several plant species (see 4.3.1.2). In their study the nutrition level was based on the foliar concentration rather than the concentration in the nutrient solution, as was done in most studies. This different reference base is undoubtedly an additional cause for the lack of agreement among the various studies.

In field studies with tobacco, Menser and Street (1962) showed that the injury severity and incidence decreased with increasing nitrogen fertilization, even though the yield increased. The authors assumed that the nitrogen fertilizer delayed leaf maturity and shortened the ozone susceptible stage. In multi-year field studies, grapes (Vitis labrusca L. cv. Concord) that were not fertilized had more photochemical oxidant injury than plants that received 56 or 112 kg N ha^{-1} (Kender and Shaulis, 1976). However, nitrogen nutrition had no influence on the response of white clover (Trifolium repens) and tall fescue (Festuca arundinacea) to long-term ozone exposures in open-top chamber (Montes _et_ _al_., 1982).

The influence of phosphorus nutrition on sensitivity of tomatoes to ozone was associated with carbohydrate content. In tomatoes grown in sand culture at three levels of phosphorus nutrition and exposed to ozone (Leone and Brennan, 1970), phosphorus-deficient plants displayed only slight injury but the injury intensity increased with the phosphorus concentration in the nutrient solution. The phosphorus-deficient plants had an elevated carbohydrate reserve prior to ozone exposure, but it decreased rapidly following exposure.

The effects of potassium nutrition on plant response are contradictory. Pinto beans and soybean beans grown at a low level of potassium exhibited more foliar injury following an ozone exposure than plants grown on a high level (Dunning _et_ _al_., 1974). The difference in sensitivity was not associated with carbohydrate content; the authors suggested that the increased injury at low potassium was associated with increased stomatal opening. Silver maple (Acer saccharinum) seedlings were grown in half-strength Hoagland nutrient solutions containing either 0, 2, or 117 ppm potassium and exposed to 0.3 ppm ozone for 6-h/day for 2 days (Noland and Kozlowski, 1979). Seedlings grown at 0 or 2 ppm potassium showed less foliar injury than plants grown at 117 ppm potassium. The increased stomatal opening that occurred in the high potassium treatment was associated with an elevated ozone uptake and more foliar injury than in the potassium-deficient plants.

At high nitrogen levels, the addition of phosphorus and potassium decreased the injury to mangel and spinach (Brewer et al., 1961). At a low soil phosphorus level, injury increased proportionally to the added potassium, but at a higher soil phosphorus level, potassium addition decreased injury. High phosphorus and/or potassium increased the injury to duckweed when the remaining nutrients were held constant at one-third the level of Hutner's solution (Craker, 1971b). In studies using various growth media, the amount of ozone-induced foliar injury in soybean depended on the concentration of N,P,K in the nutrient solution (Heagle, 1979b). Plants that received no supplemental nutrients exhibit only slight injury; the addition of moderate amount of fertilizer increased the ozone sensitivity. When higher fertilizer rates were used, the plants grew better than at moderate rates but the foliar sensitivity to ozone decreased.

Sulfur nutrition influenced plant susceptibility to ozone (Adedipe et al., 1972b). The tissue sulfate content was increased proportional to the sulfate concentration of the nutrient solution. Plants grown at a high sulfate level were more resistant to ozone injury possibly through an increase in the sulfhydryl content of the tissue.

The pH of the nutrient solution may have a significant influence on the intensity of plant injury (Yamazoe and Mayumi, 1977). The most intense foliar injury from ambient photochemical oxidants occurred on plants grown on the acidic nutrient salts, ammonium sulfate and ammonium chloride; moderate foliar injury occurred when ammonium sulfate was used with a decreased superphosphate content; and only slight injury occurred when ammonium nitrate or urea, which are essentially neutral, were used. The addition of lime raised the pH of the nutrient solution and decreased plant sensitivity. It is not clear if these changes in plant sensitivity represent a direct effect of pH or if pH altered the uptake of other elements which contribute to the changes in plant response.

There is no general agreement concerning the influence of plant nutrient supply on ozone sensitivity. However, an association between forest decline (see 5.5) and Mg and Ca deficiencies have been observed.

4.3 Significance of Internal Growth Factors on Plant Sensitivity

The influence of internal growth factors which provide the basis for differential plant responses is expressed in species, cultivar, and individual differential sensitivity which can change in conjunction with external growth conditions (see Chapter 4.2) and plant development.

4.3.1 The Influence of Developmental Stage and Leaf Age

To understand and evaluate the ontogenic differences in sensitivity, it is necessary to differentiate between the development of the individual and its organs. Both developmental phases influence the type and degree of plant reaction to a given air pollutant. The existing results allow only a fragmentary evaluation of the influence of plant developmental stage on sensitivity.

4.3.1.1 Leaf Age

Leaves, roots, fruit, and pollen are the plant organs most sensitive, either directly or indirectly, to photochemical oxidants. The most obvious visible responses occur to the chlorophyll-containing leaves which are the principal sites for autotrophic reactions, i.e., photosynthesis. The leaves or needles of higher plants are especially good indicators of the degree of air pollution from photochemical oxidants.

Analogous to other air pollutants (Guderian, 1977), the sensitivity of leaves to ozone and PAN varies substantially with leaf age. The schematic representation (Figure 14) from the work of Glater et al. (1962) illustrates these changes. Following exposure of 100 young tobacco plants to photochemical smog, only the middle-aged leaves, 1 to 5, showed foliar injury, while the fully differentiated leaf 6 and the younger expanding leaves in the apical meristem were uninjured. Zones of differential sensitivity were also observed on individual leaves. For example, the basal portion of leaf 4 displayed 87% foliar injury, while the similar position on leaf 3, the next youngest, had only 25% foliar injury.

A series of studies confirmed the high sensitivity of middle-aged leaves (Hill et al., 1970). Leaves of dicotyledonous plant species were most sensitive during the later stages of leaf enlargement (Tingey et al., 1973b), after they had passed the period of maximum enlargement rate but prior to achieving their final size (Ting and Mukerji, 1971; Townsend and Dochinger, 1974; Evans and Ting, 1974a). These data confirm the results of Ting and Dugger (1968) and Bennett (1969) in which leaves between 65 and 95% of final expansion were most sensitive to ozone. This period of maximum sensitivity corresponded with the formation of intracellular spaces and the stomata becoming functional, allowing the diffusion of gases throughout the leaf. In a few plant species, mature leaves can be injured (Shertz et al., 1980b), but young leaves are uniformly resistant to injury (Hill et al., 1970).

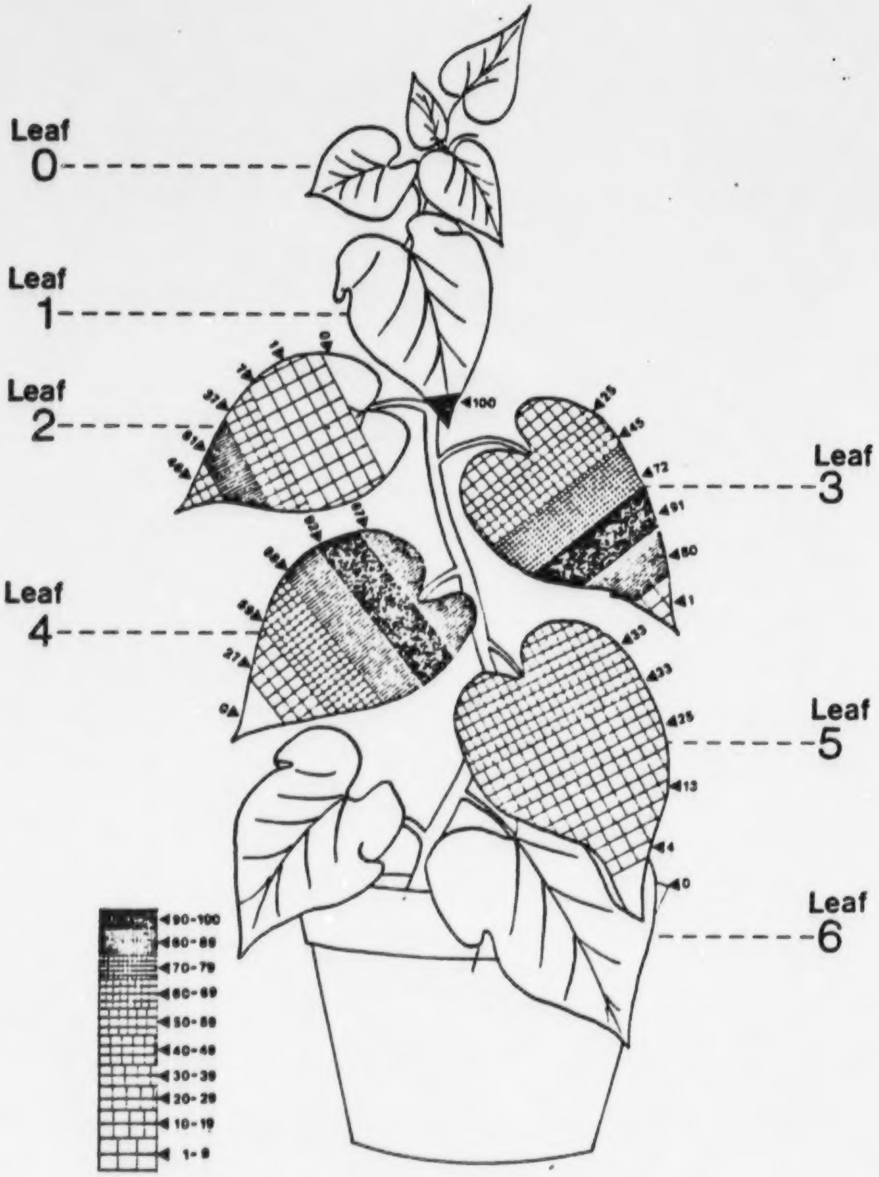
Leaf 0
Leaf 1
Leaf 2
Leaf 3
Leaf 4
Leaf 5
Leaf 6
100
25
45
72
91
80
1
33
33
25
13
4
0
27
0
90-100
80-89
70-79
60-69
50-59
40-49
30-39
20-29
10-19
1-9

Figure 14. The distribution of injury to tobacco leaves showing the influence of leaf age and leaf developmental stage on sensitivity to photochemical smog (Glater et al., 1962).

Every leaf passes through phases of differential sensitivity; however, the chronological leaf age is less important than its physiological one (Dugger and Ting, 1970a, b; Taylor, 1973c). During the course of shoot elongation and development, for plants such as tobacco and field bean (Vicia faba), the most susceptible leaf position rises from the basal leaves toward the apex. Sensitive petunia cultivars acquired a marked ozone tolerance following the visible differentiation of the flower bud and the tolerance was displayed several nodes below the flowering node (Hanson et al., 1975). Differential injury levels on leaves of individual shoots reflected the differential exposures of the preceding days, weeks, and months (Ashmore et al., 1980a), one of the values of indicator plants (see Chapter 3.2). Plants with a rosette growth habit, e.g., lettuce, celery, or beets, exhibit injury earlier on the outer rosette leaves than the inner ones during the early stages of plant development. As with sulfur dioxide (van Haut and Stratmann, 1970), leaf susceptibility is displaced toward the center of the rosettes and corresponds to the developing leaves. To assess the total effect of a single exposure, it is necessary to consider the susceptible developmental stages of the total number of leaves on the plant.

Conifer needles display an age-dependent change in susceptibility, similar to dicotyledonous plant leaves. Ponderosa pine needles that were 5 to 7 weeks old (60 to 90 mm long) and still elongating were most sensitive (Davis and Coppolino, 1974a). The susceptibility decreased as the needles reached full elongation, 100 to 120 mm. In a second similar experiment, ozone injury was the most severe on 5- to 8-week old needles (Davis, 1977). Virginia pine seedlings were exposed to 0.25 ppm ozone for 4 h; cotyledon, primary, and secondary needles were most severely injured when the needles were 3 to 5 weeks old (Davis and Wood, 1973b).

The high susceptibility of young, developing needles during early summer is not necessarily the time when the most severe injury occurs in ozone-impacted areas. With chronic exposures, the effects accumulate to a maximum toward the end of the growing season. Long term, low concentration exposures may also injure mature tissue of certain species, i.e., pine or beans (Hill _et al_., 1970).

The tissue age-dependent differences in susceptibility of various zones of the leaf (Glater _et al_., 1962; Evans, 1973) are considerable and range from symptom-free portions to variable injury severity on others. A generalization for ozone injury to dicotyledonous plants can be made: on the youngest susceptible leaves, visible injury occurs primarily on the leaf tip; on the next oldest leaves, injury occurs in the middle, and on the oldest leaves, at the base of the leaf blade (Menser _et al_., 1963; Hill _et al_., 1970). Corresponding to the progressive differentiation of the tissue, the transverse susceptibility zones shift from leaf tip to leaf base (compare Figure 13).

Conifers display a similar age-dependent relationship. During needle expansion, primarily the tips are injured (Berry and Ripperton, 1963). With increasing needle age, the zone of "recently mature" tissue migrates to the needle base (Davis and Wood, 1973b). On fully differentiated needles, injury symptoms are distributed uniformly over the needle length (Davis and Coppolino, 1974a).

The state of tissue development influenced the distribution of photochemical oxidant injury (Bobrov, 1955a). In agreement with progressive cell differentiation from leaf tip to leaf base, bifacial necrosis on half-developed annual bluegrass (Poa annua) leaves occurred on the tip of the youngest affected leaf, in the middle of the lower next oldest leaf, and at the base of the oldest leaves.

On dicotyledonous plant species such as petunia or small nettle (Urtica urens L.) and monocotyledonous species such as annual bluegrass, PAN exposure caused banding injury symptoms that corresponded to leaf development (Taylor et al., 1960; Taylor and McLean, 1970; Posthumus, 1977). At moderate PAN exposures, visible symptoms were restricted to the lower leaf surface of dicotyledonous plants because injury occurred primarily in the spongy mesophyll. PAN studies on 10 bean cultivars found that the primary leaves were more susceptible than secondary leaves (Starkey et al., 1976). According to Dugger et al. (1963b), the youngest leaves of pinto bean were most susceptible to PAN, while the more developed ones were most susceptible to ozone. However, deviations from this relationship can occur with changes in growth conditions.

After a single PAN exposure, the following sequence of injury symptoms can be observed on the leaflets of compound leaves such as tomato and potato (Taylor and McLean, 1970). Corresponding to the succession of tissue maturation, symptoms appeared at the apex of the terminal leaflet on the youngest susceptible leaf; the next oldest leaf was usually injured near the base of the terminal leaflet and at the apex of the first two lateral leaflets. The third oldest susceptible leaf was injured at the base of the first two lateral leaflets and at the apex of the second pair of lateral leaflets, while the more mature terminal leaflet remained symptomless. PAN exposures on successive days caused separate and distinct injury bands on the leaf blade. On monocotyledonous leaves, PAN symptoms appeared as distinct transverse bands from a few mm to perhaps 2 cm wide (Bobrov, 1955a; Juhren et al., 1957; Noble, 1965).

4.3.1.2 Developmental Stage

While leaf and tissue age-dependent sensitivity to photochemical oxidants has been extensively studied, only a few studies have been concerned with the sensitivity of the whole plant during the course of its development. Short-lived plants are especially sensitive to ozone during their early developmental stages. With few exceptions, 9- to 14-day old seedlings of numerous grass species were more injured by ozone (0.05 to 0.5 ppm) than 66- to 71-day old plants (Richards et al., 1980). Ozone reduced radish hypocotyl growth the most if the exposure occurred during the period of rapid hypocotyl enlargement (Tingey et al., 1973a). Hypocotyl growth was reduced 37% from a single ozone exposure to 14-day-old plants, while growth was reduced 25 and 15% in 7- and 21-day old plants, respectively. Pinto beans (Heck and Dunning, 1967) and soybeans (Blum and Heck, 1980) were most susceptible to ozone at 9 to 17 and 8 to 11 days old, respectively. Young cereal and spinach plants were generally more susceptible than mature stands (Hill et al., 1970). Sensitive sweet corn cultivars were essentially uninjured by ozone once they reached a height of 45 cm. Studies with white beans in areas impacted with photochemical oxidants indicated that crop maturity (stage of development) regulated the time of symptom expression and crop vigor its severity (Haas, 1970). Petunia hybrids became less sensitive to ozone when the flower buds differentiated (Hanson et al., 1975).

In general, the extent of foliar injury does not allow a reliable estimate of the magnitude of yield loss that will result. If the foliar injury occurs during the early developmental stages and good growth conditions prevail, the plant yield will approach or equal the yield of uninjured plants. It is not known if the later stages of cereal development -- spike emergency to the milk stage -- are "critical periods" during which ozone may have a permanent impact on yield, however, these stages are especially susceptible to SO_2- and NO_2-induced yield reductions (van Haut, 1961; van Haut and Stratmann, 1967). Wheat yield was reduced 30% from 4-h exposures of 0.20 ppm ozone for 7 days during anthesis (Shannon and Mulchi, 1974).

For woody plants, there are only limited data available concerning their resistance reactions and these are generally limited to very early developmental stages. Seedlings of four conifer species were most sensitive to ozone at age 2 weeks or younger, while for sulfur dioxide they were first sensitive after 8 weeks (Berry, 1974). Virginia pine seedlings that had cotyledonary, primary, or secondary needles were exposed to 0.25 ppm ozone for 4 h and foliar injury assessed on a scale of 1 to 7 (Davis and Wood, 1973b). All three needle types were maximally sensitive at 3 to 5 weeks following needle emergence. However, the cotyledonary needles were most severely injured (injury scale 6) with the primary and secondary needles exhibiting injury indices of 3.5 and 4, respectively. With annual plants, the cotyledonary leaf stage is the "critical developmental" for sulfur dioxide (Van Haut, 1961). Necrosis on cotyledons has a strong influence on the subsequent development of the plant.

The high susceptibility of the very early developmental stage was confirmed by Townsend and Dochinger (1974) on studies with red maple (Acer rubrum) seedlings. At the youngest growth stages (plants were 4 to 11 cm high), the plants displayed more foliar injury and larger growth reductions than seedlings in the oldest growth stages (24 to 32 cm high).

To evaluate the risk to forests, the sensitivity of individual tree and understory species during their later developmental stages needs to be understood. These are difficult studies to conduct, witness the decades of studies with sulfur dioxide. Field observations showed (Wentzel, 1963) that conifers, in the later pole to the timber stage were particularly susceptibile to sulfur dioxide; similar conditions also prevailed for mature trees. During this developmental phase, large growth reductions and disintegration of stands can occur (Wentzel, 1962; Knabe, 1970; Materna _et al_., 1969).

Three factors are suggested as possible causes for the differential sensitivity of individual leaf developmental stages to ozone and PAN:

-- differential pollutant uptake per unit leaf area per unit time;

-- differential distribution of the absorbed pollutant influencing the amount reaching the active sites within the mesophyll cells;

-- biochemically controlled differences in the susceptibility of the leaf.

As shown in Chapter 2.1, practically all photochemical oxidants reach the leaf interior by diffusion through the stomatal pore. The number, condition, and function of the stomata consequently influence the rate and amount of pollutant absorbed. At very early developmental stages of cotyledonary or foliage leaves, few functional stomata are present (Meidner and Mansfield, 1968). The lack of functional stomata or very low gas exchange explains the high "resistance" of this developmental stage to ozone and PAN. With increasing leaf age, the stomata rapidly become functional; gas exchange per unit area reaches a maximum prior to full leaf expansion and then it declines (Guderian, 1970). Intermediate-aged tobacco leaves had a higher ozone uptake rate than young or old leaves (Craker and Starbuck, 1973). Young-expanding Camellia leaves absorbed three times as much ozone as mature leaves (Thorne and Hanson, 1972). Correspondingly, differential injury in relation to leaf developmental stages results, in part, from variable polluant absorption.

The importance of stomata for pollutant uptake and response was confirmed by Evans and Miller (1972b); ozone-sensitive pine species had a higher stomatal frequency than did resistant species. Similarly, the stomatal frequency of susceptible tobacco cultivars was about 30% higher than that of resistant ones, but there was no relationship with stomatal size (Dean, 1972). In contrast, Elkiey et al. (1979) found no association between stomatal frequency or size and the differential sensitivity of various petunia cultivars. The sensitive cultivar had the lowest stomatal frequency and the largest stomatal pore size, yielding no difference in total stomatal pore area per leaf among the cultivars. However, the resistant petunia cultivar had a rougher epidermis and denser trichomes. In peas, differential cultivar response was not associated with external leaf characteristics (Dijak and Ormrod, 1982). In grapes (Vitis labrusca), an ozone-sensitive cultivar had a lower leaf conductance and fewer stomata than its resistant counterpart (Rosen et al., 1978). As soybean leaves expanded from 25 to 100% of final size, the ozone-resistant cultivar maintained a higher stomatal frequency than its susceptible counterpart (Taylor et al., 1982).

With leaf expansion and parallel to the development of functional stomata as entrance ports, intercellular spaces form which are important for pollutant distribution, as shown by Glater (1956) with her studies of ferns. Turrell (1942) associated differential sulfur dioxide responses among alfalfa (Medicago sativa) leaves to differences in the intercellular space volume and mesophyll cell-surface area. In contrast, differential ozone sensitivity of soybean cultivars was not related to internal leaf characteristics (Taylor et al., 1982). In soybean, the formation of intercellular spaces coincided with the period of rapid leaf expansion and the cessation of cell division in the palisade layers (Decker and Postlewait, 1960), which was also the developmental stage most susceptible to ozone (Tingey et al., 1973b). The reduced ozone injury in fully expanded leaves was associated with the formation of cutin and suberin layers on the mesophyll cells which in turn would reduce the penetration of ozone to its active site within the cell (Glater et al., 1962).

Differential susceptibility associated with either leaf age or plant developmental stage cannot be related solely to differential pollutant uptake and distribution within the leaf. Specific biochemical factors must also be considered.

During leaf development, the period of maximum ozone susceptibility occurred when reducing and soluble sugars were at a minimum. Studies on beans (Heath et al., 1974; Bennett et al., 1977) showed that the period of maximum leaf expansion rate coincided with a minimum sugar content and maximum ozone susceptibility. In cotton, agreement was found between the minimum soluble sugar content and maximum ozone susceptibility, which occurred after the maximum expansion rate but prior to full leaf expansion (Ting and Mukerji, 1971). Similarly, in eastern white pine needles, maximum sensitivity was related to the period of lowest sugar content (Barnes and Berry, 1969).

The relationship of additional plant metabolites to plant sensitivity has been investigated. In cotton and soybean leaves, maximum susceptibility corresponded with the minimum free amino acid content (Ting and Mukerji, 1971; Tingey et al., 1973b) and in tobacco with the minimum total protein content (MacDowall, 1965b). This highly susceptible phase corresponded with minimum concentrations of sulfhydryls (Dugger and Ting, 1970a, b), nucleotides (Leopold, 1964), and ascorbic acid (Hanson et al., 1970). A foliar application of abscisic acid reduced ozone injury through a decrease in stomatal aperture (Fletcher et al., 1972), presumably reducing ozone uptake. If these relationships are causal or only correlated are generally unresolved questions.

4.3.2 Species, Cultivar, and Individual Plant Resistance

Individual plant species, cultivars, provenances, and even individuals of populations react with differential sensitivity to given air pollutant stresses. In contrast to specific plant pathogenic organisms (Gäumann, 1951), there is no absolute resistance to air pollutants. Every plant species can be injured by appropriate combinations of pollutant concentrations and exposure duration. The relative plant resistance to air pollutants is based on the expression of genetic traits which may change during development (Dochinger et al., 1965; Taylor, 1968; Hanson et al., 1976), determining the susceptibility of individual plants. The variable tolerance of various species, cultivars, provenances, and individual plants during plant development also is determined by both previous and current environmental conditions (Figure 1) (Guderian and Küppers, 1980b).

4.3.2.1 Criteria to Evaluate Resistance

Levitt (1980) defined two mechanisms of plant resistance to stress: "stress avoidance" and "stress tolerance." In the former case, the stress induced by a specific ambient dose was partially or completely excluded. Numerous factors control the resistance of plant organs to the ingress of damaging compounds into the cells. In addition to morphological characteristics such as leaf shape, epidermal structure, including waxes and trichomes (Rentschler, 1973; Elkiey et al., 1979), stomatal number, size, distribution (Meidner and Mansfield, 1968; Evans and Miller, 1972b; Dean, 1972) and stomatal resistance are of importance (Ting and Dugger, 1971; Thorne and Hanson 1972, 1976; Turner et al., 1972; Miyake et al., 1974; Tingey and Taylor, 1982). During the course of development, the above mentioned morphological parameters adapt to changes in plant water relations. Morphological characteristics that reduce transpiration also reduce gas exchange and may thereby decrease pollutant uptake. Stress avoidance mechanisms that are effective against photochemical oxidants are known. In ozone-resistant onion cultivars, the stomata closed following injury to the guard cell membranes, while in sensitive cultivars the stomata remained open, allowing additional ozone uptake and injury (Engle and Gabelman, 1966). Similar observations were reported by Butler and Tibbitts (1979a) on various bean cultivars and by Elkiey and Ormrod (1979c, 1980a) on differentially sensitive petunia cultivars. Total leaf conductance of ozone-sensitive tobacco cultivars was greater than that of tolerant cultivars, but the differences were not sufficient to completely explain the differences in injury (Turner et al., 1972). In soybean and pea cultivars, differential susceptibility was not related to stomatal exclusion or differential stomatal closure (Taylor et al., 1982). In fact, the tolerant soybean cultivar absorbed as much or more ozone than the sensitive cultivar.

"Stress tolerance" assumes the absorption of the particular pollutant into the cells (Taylor, 1978a). When the absorbed material is assimilated, tolerated, or buffered, no morphological or physiological change ("strain") occurs and "strain avoidance" exists. Above a specific intracellular concentration, that is to say, when biochemical thresholds are exceeded, injury occurs which is either reversible (elastic strain), i.e., subtle changes in the photosynthetic rate, or irreversible (plastic strain), i.e., leaf necrosis. Following perturbations, living systems attempt to reestablish normal metabolic states through repair and/or compensatory processes for the perturbation and its consequences (Levitt, 1980; Tingey and Taylor, 1982). Repair processes remedy the cellular perturbation, removing the cellular dysfunction. However, with compensation, the perturbation and its physiological consequences remain but the cell responds with mechanisms that counter the detrimental effects. Recovery from the perturbation or dysfunction may range from partial to complete and consequently injury will vary as well.

Biochemical thresholds characterize the transition between strain avoidance and strain tolerance as well as elastic strain and plastic strain and determine the tolerance of individual plants. From this explanation, it follows that the individual responses can be expressed as changes in or the death of the affected plant, subject to the intensity of the ambient stress and the actual resistance of the plant.

Recently, Tingey and Taylor (1982) proposed a conceptual model to explain the causes of environmental, developmental, and genetically controlled differences in plant responses to ozone. The model (Chapter 2) proposed that plant injury resulted from ozone diffusion to susceptible sites within the cells and that three general processes controlled the magnitude and expression of the injury:

-- processes that controlled the flux of gases into the leaves

-- processes that influenced pollutant distribution with the leaf, including ozone-scavenging reactions

-- processes that repaired or compensated for the perturbation

The active interplay of these processes controlled the amount of injury; the relative importance of the processes varied among plants and was influenced by internal and external conditions.

The basis for the genetically controlled differences in resistance to ozone and PAN is, in general, not resolved. However, in addition to the role of gas absorption and distribution, various plant metabolites and metabolic scavenging or repair reactions have been suggested.

Cultivar differences in sensitivity have been associated with differences in soluble sugars, including reducing sugars, as have developmental differences (see Chapter 4.3.1.2), but the mechanism of the increased tolerance is not known. The older leaves of the ozone-insensitive tobacco cultivar Bel B contained a significantly lower soluble sugar content than the older leaves of the ozone-sensitive 'Bel W_3' (Dugger _et al._, 1966). In contrast, the young ozone insensitive leaves of both cultivars exhibited similar high sugar concentrations.

Differential foliar concentrations of ascorbic acid were correlated with the oxidant sensitivity of petunia cultivars (Hanson _et al._, 1970, 1971). The exogenous application of ascorbic acid to isolated chloroplasts decreased the effect of PAN on photosynthesis (Dugger and Ting, 1970b). In plant cells, ascorbic acid functions as a reducing compound with absorbed sulfur dioxide (Keller and Schwager, 1977) and a weak oxidizing agent with PAN and ozone (Mudd, 1980). However, ascorbic acid may not have a general role in plant resistance to photochemical oxidants. Differentially susceptible tobacco and petunia cultivars exhibited no differences in their foliar ascorbic acid contents (Menser, 1964; Thorne and Hanson, 1976). An oxidant exposure decreased the foliar concentration of ascorbic acid in petunia leaves (Hanson et al., 1970) but caused no change in ascorbic acid content of ponderosa pine seedlings following chronic ozone exposures (Miller et al., 1969).

The chemical reactivity of ozone in the liquid phase within the cell may affect its movement and distribution. Ozone may react with unsaturated fatty acids, sulfhydryl and ring-containing compounds or various scavenging systems (see 2.1.1.2).

The role of sulfhydryl compounds in the expression of variable resistance is unclear. Ozone and PAN react preferentially with sulfhydryl compounds, oxidizing them to disulfides and sulphonic acids (Tomlinson and Rich, 1970); Mudd and Freeman, 1977; Freeman et al., 1979). Sulfhydryl compounds, particularly SH enzymes, have various functions in cellular metabolism, and their reduction or inactivation will be reflected in a corresponding loss of function. Tobacco cultivars insensitive to ozone contained lower levels of sulhydryls and ATP than sensitive cultivars (Tomlinson and Rich, 1968). The significance of the total sulfhydryl content in relation to sensitivity is unclear; the deciding factor may be the function of the sulfhydryl compounds and whether they are increased or decreased.

Plant species or cultivars which displayed extensive foliar necrosis following ozone exposure produced more polyphenols, which following oxidation by peroxidases and polyphenol oxidases to quinones can polymerize with amino acids and proteins (Howell, 1974). These enzymes were activated sooner and to a higher level in sensitive soybean cultivars than resistant ones (Tingey et al., 1976a). However, in differentially sensitive pea cultivars, leaf peroxidase activity increased about the time foliar injury was visible but it was unrelated to cultivar sensitivity (Dijak and Ormrod, 1982).

In addition to genetic factors, differential responses are influenced by developmental stage (see 4.3.1), edaphic and climatic factors (see 4.2), and biological interactions (see 2.5). The moderating effect of environmental factors before, during, and after pollutant response are, in part, responsible for the striking deviations in the relative resistance listings and groupings proposed by various authors. However, the genetic and environmentally controlled sensitivity relations of plant species, cultivars, and individuals provide an important basis for practical measures for environmental protection. If these relationships are optimally used for diagnostic purposes, planting recommendations for pollution-impacted areas, the breeding and selection of relatively resistant cultivars, and the determination of dose-response relationships, then, in addition to the previously discussed factors, the selected response criteria and the concentrations of ozone and PAN must be considered when establishing and evaluating the degree of relative sensitivity.

The studies of Heagle (1979a) using various ozone concentrations on soybean cultivars confirmed the observation that plant sensitivity depended on pollutant concentration (Wentzel, 1963; Tingey et al., 1972). With chronic ozone exposures, soybean cultivars displayed a different susceptibility sequence than with high, acutely injurious concentrations. The importance of the response criteria used to determine relative resistance was also emphasized (Heagle, 1979a). When visible injury was used to evaluate differential susceptibility, the soybean cultivars exhibited a different sensitivity ranking than when production was used. Jensen (1973) reached a similar conclusion during his studies of the sensitivity relationships of various deciduous trees. In many species, foliar injury is not always correlated with plant yield. Also, sensitivity rankings based on foliar injury are not always the same as those based on yield (e.g., Oshima _et al._, 1977). In only a few cases has the relative resistance determined by visible injury (Wood and Coppolino, 1972) agreed with that determined by growth. It is preferable to determine relative resistance based on the reduced performance of the affected species; the function of the plant species in question should determine the criteria used to evaluate the response (Guderian, 1977).

Only in recent years have there been comprehensive studies of the criteria used to assess relative plant resistant to photochemical oxidants. Following the considerations of Kulagin (1973), Harkov and Brennan (1979) proposed the consideration of an ecophysological perspective for the evaluation and determination of the ozone sensitivity of deciduous trees in the northeastern USA. The inclusion of, or example, rate and dynamics of growth (Jensen, 1973), reproduction (Harward and Treshow, 1975; Smith, 1980), and the position of the species in plant succession (Miller and McBride, 1975) in resistant evaluations provides a reference point from which to evaluate the possible survival of trees in oxidant-impacted areas. Comparative studies of the resistance relations of the same species and cultivars in controlled pollutant exposures and in ambient-pollutant impacted areas provide an additional opportunities to obtain reliable results (Karnosky, 1978).

The available sensitivity groupings are based primarily on the use of visible symptoms as response criteria. In addition, the majority of the studies used short-term pollutant exposures to acute injurious concentrations of ozone and PAN, therefore caution is required before using these data to estimate the risk to a plant species or its suitability for growing in photochemical oxidant impacted locations.

4.3.2.2 Relative Ozone Sensitivity

Table 10 contains a synopsis of the relative sensitivity of shrubs, ornamentals, coniferous, and deciduous trees to ozone. In developing the listing of sensitive, intermediate, and less sensitive species, Davis and Wilhour (1976) used results from controlled ozone exposures as well as observations from the field. They indicated that their listing was not only a compilation of earlier research, but also contained new unpublished results.

Table 10. Relative Ozone Sensitivity of Woody Plants Grown in North America (Davis and Wilhour, 1976)

Sensitive Species:

- Ailanthus, tree-of-heaven (*Ailanthus altissima*, Swingle)
- Ash, European mountain (*Sorbus aucuparia* L.)
- Ash, green (*Fraxinus pennsylvanica* Marsh.)
- Ash, white (*Fraxinus americana* L.)
- Azalea, campfire (*Rhododendron kaemphri* 'Campfire' [Planch] Wils. Hort.)
- Azalea, Hinodegiri (*R*. *obtubsum Planch*. 'Hinodegiri')
- Azalea, Korean (*R*. *poukhanensis* Leville)
- Azalea, snow (*R*. *kurume* 'snow' [Rehd.] Hort.)
- Bridalwreath (*Spirea vanhoutii*)
- Cherry, Bing (*Prunus avium* var. Bing)
- Cotoneaster, rock (*Cotoneaster horizontalis* Decne.)
- Cotoneaster, spreading (*C*. *divaricata* Rend. and Wils.)
- Grape, Concord (*Vitis vinifera*)
- Honey locust (thornless) (*Gleditsia triacanthos inermis* [L.] Zebel.)
- Larch, European (*Larix decidua* Mill)
- Lilac, Chinese (*Syringa chinensis*)
- Oak, Gambel (*Quercus gambelii*)
- Oak, white (*Quercus alba* L.)
- Pine, Austrian (*Pinus nigra* Arnold)
- Pine, jack (*Pinus banksiana* Lamb.)
- Pine, Jeffrey (*Pinus jeffreyi*)
- Pine, Loblolly (*Pinus taeda*)
- Pine, Monterey (*Pinus radiata*)
- Pine, ponderosa (*Pinus ponderosa* Laws.)
- Pine, Virginia (*Pinus virginiana* Mill.)
- Poplar, hybrid-mixed (*Populus maximowiczii* x *trichocarpa*)
- Poplar, tulip (*Liriodendron tulipifera* L.)
- Privet, londense (*Liqustrum vulgare* var. pyamidale)
- Serviceberry, Saskatoon (*Amelanchier anifolia*)
- Snowberry alba (*Symphoricarpos alba*)

(continued)

Table 10 (continued)

Sumac fragrant (*Rhus aromatica*)
Sycamore, American (*Platanus occidentalis* L.)
Walnut, English (*Juglans regia*)

Intermediate Species:
Apricot, Chinese (*Prunus armeniace* var. Chinese)
Boxelder (*Acer negundo*)
Cedar, incense (*Libocedrus decurrents*)
Cherry, Lambert (*Prunus avium* var. Lambert)
Current, northern black (*Ribes hudsonianum*)
Elder, black bead (*Sambucus melanocarpa*)
Elm, Chinese (*Ulmus parvifolia* Jacq.)
Forsythia, Lynwood Gold (*Forsythia intermedia spectabilis* 'Lynwood Gold' Koehn)
Gum, sweet (*Liquidambar styraciflua* L.)
Hemlock, eastern (*Tsuga canadensis* [L.] Cart.)
Larch, Japanese (*Larix leptolegis* [Sieb. and Fucc.] Gord.)
Mock Orange, sweet (*Philadelphus coronarius* L.)
Oak, black (*Quercus velutina*)
Oak, pin (*Quercus palustris* Muenchh.)
Oak, scarlet (*Quercus coccinea* Muenchh.)
Pine, eastern white (*Pinus strobus* L.)
Pine, lodgepole (*Pinus contorta*)
Pine, pitch (*Pinus rigida* Mill.)
Pine, scotch (*Pinus sylvestris* L.)
Pine, shortleaf (*Pinus echinacta*)
Pine, slash (*Pinus elliottii*)
Pine, sugar (*Pinus lambertiana*)
Pine, Torrey (*Pinus torreyana*)
Privet, common (*Ligustrum vulgare*)
Redbud, eastern (*Cercis canadensis* L.)
Rhododendron (*Rhododendron catawbiense album* [Wichx.] Hort.)
Rhododendron (*Rhododendron nova zembla* Hort.)
Rhododendron (*Rhododendron roseum elegans* Hort.)

(continued)

Table 10 (continued)

Snowberry, vaccinioides (*Symphoricarpos vaccinioides*)
Viburnum, linden (*Virburnum dilatatum* Thunb.)
Viburn, Tea (*Viburnum setigerum* Hance.)

Less Sensitive Species:
Apricot (*Prunus aremeniaca*)
Arborvitae (*Thuja occidentalis* L.)
Azalea, Chinese (*Rhododendron mollis* Ll.)
Avocado (*Persia americana*)
Beech, European (*Fagus sylvatica*)
Birch, European white (*Betula pendula* Roth.)
Box, Japanese (*Buxus sempervirens*)
Dogwood, gray (*Cornus racemosa* Lam.)
Dogwood, white (*Cornus florida* L.)
Euonymus, dwarf winged (*Euonymus alatus compactus* [Sieb.] Bailey)
Fir, balsam (*Abies balsamea* [L.] Mill.)
Fir, Douglas (*Pseudotsuga menziesii* [Mirb.] Frenco.)
Firethorne, Laland's (*Pyracantha coccinea laland* Depp.)
Gum, black (*Nyssa sylvatica* [Marsh.] Pepperidge)
Holly, American [female and male] (*Ilex opaca* Ait.)
Holly, Hetz Japanese (*Ilex crenata Hetzi* [Thunb.] Hetzii.)
Holly, English (*Ilex aquifolium*)
Juniper, western (*Juniperus occidentalis*)
Laurel, mountain (*Kalmia latifolia* L.)
Linden, American (*Tilia americana* L.)
Linden, little-leaf (*Tillia cordata* Mill.)
Locust, black (*Robinia pseudoacacia*)
Mahonia, creeping (*Mahonia repens*)
Maple, bigtooth (*Acer grandidentatum*)
Maple, Norway (*Acer platanoides* L.)
Maple, sugar (*Acer saccharum* Marsh.)
Oak, bur (*Quercus macrocarpa*)
Oak, English (*Quercus robur* L.)
Oak, northern red (*Quercus rubra* L.)

(continued)

Table 10 (continued)

Oak, shingle (*Quercus imbricaria* Michx.)
Oregon Boxwood (*Pachistina myrsinites*)
Pagoda, Japanese (*Sophora japonica*)
Peach (*Prunus persica*)
Pear, bartlett (*Pyrus communis* var. Bartlett)
Pieris, Japanese (*Pieris japonica* [Thunb.] D. Don)
Pine, digger (*Pinus sabiniana*)
Pine, singleleaf pinyon (*Pinus monophylla*)
Pine, red (*Pinus resinosa* Ait.)
Privet, Amur north (*Liquistrum amurense* Carr.)
Redwood (*Sequoa sempervirens*)
Rhododendron, Carolina (*Rhododendron carolinianum* Redh.)
Sequoia, giant (*Sequoia gigantea*)
Spruce, Black Hills (*Picea glauca* var. *densata* Bailey)
Spruce, Colorado blue (*Picea pungens* Engelm.)
Spruce, Norway (*Picea abies* [L.] Karst.)
Spruce, white (*Picea glauca* [Moench] Voss.)
Viburnum, Korean spice (*Viburnum carlesi* Hens.)
Viburnum, burkwoodii (*Viburnum burkwoodii*)
Wood's rose (*Rosa woodsii*)
Yew, dense (*Taxus densiformis* Hort.)
Yew, Hatfield's pyramidal (*Taxus media hatfieldi* Rend.)

NOTE

To prevent the misunderstanding that there is an absolute ozone resistance the term "less sensitive" rather than "tolerant" is used. Within a sensitivity grouping, species are arranged alphabetically by common name.

The previous table illustrated that numerous economically and ecologically important woody plant species exhibited sensitive and intermediate sensitive reactions to ozone, in contrast to PAN. In addition, various species important to European agriculture, i.e., grapes, fruit tree crops: Cherry-sweet, walnut and currants; forest species: European and Japanese Larch, Scotch pine and Austrian pine are ozone sensitive. Notable is the relative ozone tolerance of European beech and Norway spruce which are among the most sensitive tree species to sulfur dioxide and hydrogen fluoride (Wentzel, 1968). There is also a wide range in relative sensitivity among individual species within a genus, i.e., Quercus and Pinus which have species in all three sensitivity groupings. It is not possible to establish a clear difference in relative ozone sensitivity between coniferous and deciduous trees as it is for the acidic gases, SO_2 and HF.

The relative ozone sensitivity of agricultural crops and weeds listed in Table 11 is based on the handbook, "Diagnosing Vegetation Injury Caused by Air Pollution" (EPA, 1976).

Table 11. Relative Sensitivity of Agricultural Crops and weeds to Ozone (EPA, 1976)

Sensitive Species:

- Alfalfa (*Medicago sativa* L.)
- Barley (*Hordeum vulgare*)
- Bean (*Phaseolus vulgaris*)
- Buckwheat (*Fagopyrum vulgaris*)
- Citrus (*Citrus* sp.)
- Clover, red (*Trifolium pratense* L.)
- Corn, sweet (*Zea mays* L.)
- Grape (*Vitis vinifera* L.)
- Grass, bent (*Agrostis palustris* Huds.)
- Grass, brome (*Bromus inermis* L.)
- Grass, orchard (*Dactylis glomerate* L.)
- Muskmelon (*Cumunis melo* L.)
- Oat (*Avena sativa* L.)
- Onion (*Allium cepa* L.)
- Potato (*Solanum tuberosum* L.)
- Radish (*Raphanus sativus* L.)
- Rye (*Secale cereale*)
- Safflower (*Carthanus tintoiius* L.)
- Smartweed (*Polygonum* sp.)
- Soybean (*Glycine max* [L.] Merr.)
- Spinach (*Spinacia oleracea* L.)
- Tobacco (*Nicotiana tabacum* L.)
- Tomato (*Lycopersicon esculentum* Mill.)
- Wheat (*Triticum aestivum* L.)

Intermediate Species:

- Cabbage (*Brassica oleracea* L.)
- Carrot (*Daucus carota* L.)
- Corn, field (*Zea mays* L.)
- Cowpea (*Vigna sinensis* Savi)
- Cucumber (*Cumunis sativus* L.)
- Endive (*Cichorium endivia* L.)

(continued)

Table 11 (continued)

Hypericum (*Hypericum* sp.)
Parsley (*Petroselinum crispum* NYM)
Parsnip (*Pastinaca sativa* L.)
Pea (*Pisum sativum*)
Pepper (*Capsicum frutescens* L.)
Peanut (*Arachis hypogaea*)
Sorghum (*Sorghum vulgare*)
Stevia (*Pigueria trivervia* Cav.)
Timothy (*Phleum pratense* L.)
Turnip (*Brassica rapa* L.)

Less Sensitive Species:
Beet (*Beta* sp.)
Cotton (*Gossycium* sp.)
Descurainia (*Descurainia californica* [Gray] Schultz)
Jerusalem cherry (*Solanum pseudo-capsicum* L.)
Lamb's quarters (*Chenopodium album* L.)
Lettuce (*Lactuce sativa* L.)
Mint (*Mentha* sp.)
Piggy-back plant (*Tolmiea menziesii* Torr. and Gray)
Rice (*Oryza sativa* L.)
Strawberry (*Fragaria* sp.)
Sweet potato (*Ipomoea batatas* L.)

NOTE

To prevent the misunderstanding that there is an absolute ozone resistance the term "less sensitive" rather than "tolerant" is used. Within a sensitivity grouping, species are arranged alphabetically by common name.

Among the important agricultural crops that are endangered by ozone are the principal cereal crops; wheat, rye, barley, oats, and the forage crops; alfalfa and red clover and vegetable crops; potato and tomato. Endive and cabbage species exhibit a relatively high ozone sensitivity in contrast to their low level of sensitivity to SO_2 and HF.

4.3.2.3 Relative PAN Sensitivity

In comparison to ozone, the lesser importance of PAN, as a phytotoxic air pollutant, is reflected by the limited number of investigations into relative plant sensitivity. In spite of similar active sites within the leaf mesophyll for ozone and PAN, considerable differences in relative plant sensitivity to the two pollutants occur both within and among species. For example, the sensitivity rankings determined for 10 bean cultivars were different for PAN and ozone (Starky _et_ _al_., 1976).

The woody plants that have been studied consistently show a high degree of "tolerance" to visible PAN injury. In the sensitivity lists of Davis and Wilhour (1976) as well as the EPA publication "Diagnosing Vegetation Injury Caused by Air Pollution" (1976), no woody plants are found under the listings of sensitive or intermediate plants (Table 12). PAN endangers primarily agricultural, horticultural and many herbaceous ornamental species (Tables 12 and 13). Sensitive responses are exhibited by the cultivated plants, i.e., oats, beans, tomatoes, lettuce, and clover; and intermediate sensitivity is shown by wheat, barley, sugar beet, and spinach. Pronounced SO_2 and HF resistance are exhibited by carrot (Guderian and Stratmann, 1968) but it displays an intermediate PAN sensitivity, again showing how the same plant may be influenced differentially by the various atmospheric components.

Table 12. The Relative PAN Sensitivity of Ornamentals and Trees (EPA, 1976)

Sensitive Species:

- Aster (*Aster* sp.)
- Dahlia (*Dahlia* sp.)
- Fuchsia (*Fuchsia* sp.)
- Mimulus (*Minulus* sp.)
- Mint (*Menta* sp.)
- Petunia (*Petunia* sp.)
- Primrose (*Primula* sp.)
- Ranunculus (*Ranunculus* sp.)
- Sweet-Basil (*Ocimum basilicum*)

Less Sensitive Species:

- Apple (*Malus sylvestris* Mill.)
- Arborvitae (*Thuja orientalis*)
- Ash, green (*Fraxinus pennsylvanica* Marsh.)
- Ash, white (*Fraxinus americana* L.)
- Azalea, campfire (*Rhododendron* sp.)
- Basswood (*Tilia americana*)
- Begonia (*Begonia* sp.)
- Birch, European white (*Betula pendula*)
- Bromiliads
- Cactus (*Cactaceae* sp.)
- Calendula (*Calendula* sp.)
- Camellia (*Camellia* sp.)
- Carnation (*Dianthus caryophyllus* sp.)
- Chrysanthemum (*Chrysanthemum* sp.)
- Coleus (*Coleus* sp.)
- Cyclamen (*Cyclamen* sp.)
- Dogwood (*Cornus florida*)
- Fir, balsam (*Abies balsamea* [L.] Mill.)
- Fir, Douglas (*Pesudotsuga menziesii* [Mirb.] Frenco.)
- Fir, white (*Abies concolor* [Gord and Glend.] Lindl.)
- Gum, sweet (*Liquidambar styraciflua*)

(continued)

Table 12 (continued)

Hemlock, eastern (*Tsuga* *canadensis*)
Ivy (*Hedera* sp.)
Larch, European (*Larix* *decidua*)
Larch, Japanese (*Larix* *leptolepis*)
Lilac, common (*Syringa* *vulgaris*)
Lily (*Lilium* sp.)
Locust, honey (*Gleditsia* *triacanthos* L.)
Maple, Norway (*Acer* *platanoides*)
Maple, silver (*Acer* *saccharinum*)
Maple, sugar (*Acer* *saccharum*)
Mountain-ash, American (*Sorbus* *americana*)
Narcissus (*Narcissus* sp.)
Oak, English (*Quercus* *robur*)
Oak, northern red (*Quercus* *rubra*)
Oak, pin (*Quercus* *palustris*)
Oak, white (*Quercus* *alba*)
Orchids (*Orchidaceae* sp.)
Perwinkle (*Vince* *minor* L.)
Pine, Austrian (*Pinus* *nigra*)
Pine, eastern white (*Pinus* *strobus*)
Pine, red (*Pinus* *resinosa* Ait.)
Pine, Scotch (*Pinus* *sylvestris*)
Poplar, hybrid (*Populus* *maximowiezii* x *tichocarpa*)
Poplar, tulip (*Liriodendron* *tulipifera*)
Spruce, Black Hills (*Picea* *glauca* *densata*
Spruce, blue (*Picea* *pungens*)
Spruce, Norway (*Picea* *abies*)
Spruce, white (*Picea* glauca)

NOTE

To prevent the misunderstanding that there is an absolute ozone resistance the term "less sensitive" rather than "tolerant" is used. Within a sensitivity grouping, species are arranged alphabetically by common name.

Table 12 (continued)

Hemlock, eastern (*Tsuga canadensis*)
Ivy (*Hedera* sp.)
Larch, European (*Larix decidua*)
Larch, Japanese (*Larix leptolepis*)
Lilac, common (*Syringa vulgaris*)
Lily (*Lilium* sp.)
Locust, honey (*Gleditsia triacanthos* L.)
Maple, Norway (*Acer platanoides*)
Maple, silver (*Acer saccharinum*)
Maple, sugar (*Acer saccharum*)
Mountain-ash, American (*Sorbus americana*)
Narcissus (*Narcissus* sp.)
Oak, English (*Quercus robur*)
Oak, northern red (*Quercus rubra*)
Oak, pin (*Quercus palustris*)
Oak, white (*Quercus alba*)
Orchids (*Orchidaceae* sp.)
Perwinkle (*Vince minor* L.)
Pine, Austrian (*Pinus nigra*)
Pine, eastern white (*Pinus strobus*)
Pine, red (*Pinus resinosa* Ait.)
Pine, Scotch (*Pinus sylvestris*)
Poplar, hybrid (*Populus maximowiezii* x *tichocarpa*)
Poplar, tulip (*Liriodendron tulipifera*)
Spruce, Black Hills (*Picea glauca densata*
Spruce, blue (*Picea pungens*)
Spruce, Norway (*Picea abies*)
Spruce, white (*Picea* glauca)

NOTE

To prevent the misunderstanding that there is an absolute ozone resistance the term "less sensitive" rather than "tolerant" is used. Within a sensitivity grouping, species are arranged alphabetically by common name.

Table 13. Relative PAN Sensitivity of Agricultural Plants and Weeds (EPA, 1976)

Sensitive Species:

- Bean (*Phaseolus vulgaris* L.)
- Celery (*Apium graveolens* L.)
- Chard, Swiss (*Beta vulgaris cicla* L.)
- Chickweed (*Stellaria media*)
- Clover (*Trifolium* sp.)
- Endive (*Cichorium endivia* L.)
- Grass, annual blue (*Poa annua* L.)
- Ground cherry (*Prunus fruticosa*)
- Jimson-weed (*Datura stranonium* L.)
- Lettuce (*Lactuca sativa* L.)
- Mustard (*Sinapis* sp.)
- Nettle, littleleaf (*Urtica urens* L.)
- Oat (*Avena sativa*)
- Pepper (*Capsicum frutescens* L.)
- Pigweed (*Amaranthus retroflexus* L.)
- Tomato (*Lycopersicon esculentum* Mill.)
- Wild-oat (*Avena sativa* L.)

Intermediate Species:

- Alfalfa (*Medicago sativa* L.)
- Barley (*Hordeum vulgare* L.)
- Beet, sugar (*Beta vulgaris* L.)
- Beet, table (*Beta vulgaris* L.)
- Carrot (*Daucus carota* L.)
- Cheeseweed (*Malva parviflora* L.)
- Dock, sour (*Rumex crispus* L.)
- Lamb's-quarters (*Chenopodium album* L.)
- Soybean (*Glycine max* [L.] Merr.)
- Spinach (*Spinacia oleracea* L.)
- Tobacco (*Nicotiana tabacum* L.)
- Wheat (*Triticum aestivum* L.)

(continued)

Table 13 (continued)

Less Sensitive Species:

- Bean, lima (*Paseolus limensis* Macf.)
- Broccoli (*Brassica oleracea* L.)
- Cabbage (*Brassice oleracea* L.)
- Cauliflower (*Brassica oleracea botytris*)
- Corn (*Zea mays* L.)
- Cotton (*Gossypium* sp.)
- Cucumber (*Cucumis sativis* L.)
- Onion (*Allium cepa* L.)
- Radish (*Raphanus sativus* L.)
- Rhubarb (*Rheum rhaponticum* L.)
- Sorghum (*Sorghum vulgare* Pers.)
- Squash (*Cucurbita pepo* L.)
- Strawberry (*Fragraria* sp.)

NOTE

To prevent the misunderstanding that there is an absolute ozone resistance the term "less sensitive" rather than "tolerant" is used. Within a sensitivity grouping, species are arranged alphabetically by common name.

4.3.2.4 Differential Cultivar Sensitivity

Differential ozone responses exist not only among individual species but also among cultivars of a single species and thus is genetically based. An extensive literature documents differential cultivar sensitivity. Selected examples will be used to illustrate the range in differential cultivar resistance and its use as a practical control measure to reduce ozone injury. In addition, the differential cultivar response data provides a general framework to extend our understanding of plant resistance to ozone.

The relative sensitivity of tobacco cultivars has been extensively examined. Heggestad et al. (1964) clearly established the differential sensitivity of six tobacco cultivars to ozone and photooxidants in California and Washington, D.C. The investigations of MacDowall et al. (1963) found that "White Gold" was the most sensitive cultivar of the 32 examined. Heggestad and Menser (1962) selected, from breeding trials with cigar-wrapper tobacco cultivars, Bel-W_3 as a highly sensitive indicator plant for ozone. Since then, this cultivar has achieved worldwide success in identifying and monitoring ozone impacted areas (Knabe et al., 1973; Jacobson and Feder, 1974; Floor and Posthumus, 1977; Ashmore et al., 1980a).

Large differences in the relative sensitivity of bean (Phaseolus vulgaris L.) cultivars were identified by the research of Davis and Kress (1974), among others. The most sensitive of the 10 cultivars examined exhibited approximately 33% leaf area injured while the least sensitive cultivar displayed only a trace of foliar injury. In this study and others, the white-flowered cultivars were more sensitive than those with colored flowers. Similar or larger differences in susceptibility were found in both controlled fumigations (Beckerson _et_ _al_., 1979) and field trials with bean cultivars in New Brunswick, New Jersey (Brennan and Rhoads, 1976). When the most sensitive cultivars were severely injured, the less sensitive cultivars were symptomless. Worthy of note was the additional observation that cultivars that exhibited the most susceptibility to ozone were the most resistant to the bean rust (Uromyces phaseoli). In similar studies, Manning and Vardaro (1974a) found only partial agreement with Brennan and Rhoads (1976) in the relative sensitivities of the various bean cultivars, possibly because of differences in growth conditions or variable high oxidant exposures.

Other research established that soybean cultivars exhibited substantial differences in cultivar susceptibility (Miller _et_ _al_., 1974; Howell _et_ _al_., 1976). The research of Heagle (1979b) with four soybean cultivars established that the relative ozone sensitivity changed with the growth medium, fertilizer rate, hour and season of exposure.

The far-reaching, frequent occurrence of injury on potato in the eastern United States and yield reductions approaching 50% (Heggestad, 1970; Heggestad, 1973) was the motivativation for extensive research on the differential sensitivity of potato cultivars (Rich and Hawkins, 1970; Brasher _et_ _al_., 1973; Heggestad, 1973). Despite deviations among individual experiments, the later maturing cultivars were generally less susceptible than the early ones (Mosley _et_ _al_., 1978). There is no clear relationship between the extent of leaf injury and the magnitude of yield reduction. However, there is undoubtedly an upper limit of injury to potato foliage beyond which yield losses will occur. The timing of ozone exposure in relation to the stage of tuber development is a significant factor influencing final production.

Hanson et al. (1976) studied the differential sensitivity of seven inbred petunia lines and showed that the degree of ozone resistance did not coincide with the level of PAN resistance. The genes responsible for oxidant resistance act in an additive manner with evidence for partial dominance in the progeny. A high degree of inheritance for resistance and susceptibility to acute ozone injury in sweet corn leaves under field conditions was shown during 2 and 3 generations of breeding with 3 series of cultivars (Cameron, 1975).

Long-term exposures of corn to ozone concentrations of 0.05 and 0.10 ppm for 7-h per day, under conditions simulating the natural environment yielded clear differences in the susceptibility of the two cultivars investigated (Heagle et al., 1972). The less sensitive cultivar "White Midget" displayed no visible injury and biomass production and yield were not significantly decreased although there was a trend toward reduced seed yield. However, the yield of the sensitive cultivar "Golden Midget" was significantly reduced at 0.10 ppm ozone. With many plant species, the reproductive stage of development appears to be more sensitive than the vegetative stage. In another study using a different corn cultivar "Coker 16," the threshold ozone doses for foliar injury and effects on growth were much lower than those for decreased kernel yield, demonstrating that field corn can withstand some injury with no yield loss (Heagle et al., 1979c). Tomatoes exposed to SO_2 (Guderian and Stratmann, 1968) or ozone (Henderson and Reinert, 1979) displayed the same relation between injury and growth. In "open-top" field-chamber exposure studies using five open pedigree and six commercial corn hybrids, large differences in cultivar resistance were found with reductions in shoot fresh weights ranging between 2 and 63% (Heagle et al., 1979c).

In investigations with many grass species and cultivars (Richards et al., 1980), the 'warm-season entries' Zoysia japonica Steud. and "Tufcote" Bermudagrass (Cynodon dactylon [L.] Pers.) were found to be less sensitive than the 'cool-season entries' such as tall fescue (Festuca arundinacea Schreb.), perennial rye grass (Lolium perenne L.), red fescue (Festuca rubra L.), Kentucky bluegrass (Poa pratensis L.), and annual bluegrass (Poa annua L.). Substantial differences in sensitivity were found among the seven cultivars of Kentucky bluegrass.

Additional information on the differential sensitivity of various agricultural and horticultural crops to ozone is available and includes, among others, investigations with cereal species (Reinert, 1975; Heagle et al., 1979e; Nakamura and Ota, 1977), forage legumes (Brennan et al., 1969; Howell et al., 1971), sugar beet (Menser, 1974), spinach (Manning et al., 1972), radishes (Reinert et al., 1972), tomato (Clayberg, 1971, 1972; Reinert and Henderson, 1980), celery (Proctor and Ormrod, 1977), chrysanthemums (Brennan and Leone, 1972; Klingaman and Link, 1975), azalea (Gesalman and Davis, 1978), petunia (Uhring, 1978), and grapes (Shertz et al., 1980a).

Among the numerous studies concerning the differential sensitivity of woody plants, the following work of Townsend and Dochinger (1974) is an example. Red maple (Acer rubrum) seedlings reacted differently to ozone depending on their provenances and the phenological stages studied. The stability of ozone tolerance during several plant and leaf ontogenic stages suggests strong genetic control which should facilitate the selection of ozone-tolerant lines.

The ozone injury threshold for five clones of quaking aspen (Populus tremuloides) varied between 0.05 and 0.20 ppm (Karnosky, 1976), additional evidence that intraspecific variation in relative resistance can be as large or larger than the interspecific variation. The occurrence of cultivars from several species in all three relative resistance rankings (sensitive to less sensitive) documents this quite clearly.

The considerable differences in the sensitivity of individuals within a species (Skelly *et al*., 1977; Blanchard *et al*., 1979; Steiner and Davis, 1979) is clearly shown by the early research on the chlorotic dwarf syndrome of eastern white pine. Scions from mother trees displaying the chlorotic dwarf syndrome exhibited the same symptoms when grafted onto healthy root stock, while scions from trees without the disease remained healthy when grafted onto the root stock of trees showing the chlorotic dwarf syndrome (Dochinger *et al*., 1965; Dochinger and Seliscar, 1965). Because of the similarity in morphology and anatomy, the genetic control of specific biochemical properties associated with differential resistance should be investigated. Coyne and Bingham (1981) measured the differential effects of ozone on the photosynthetic performance of individual ponderosa pine in relation to ecotypes.

In addition to the previously cited articles, the following publications contain extensive reviews of relative plant resistance to photooxidants (U.S. Department of Health, Education and Welfare, 1970; Linzon *et al*., 1975; Heck *et al*., 1977b; EPA, 1978a; Skelly and Johnson, 1979).

4.4 Measures to Reduce Pollutant Effects in Plant Stands

The principal means of protecting vegetation from photochemical oxidants injury is by reducing the precursors of photochemical oxidants, thereby reducing the ambient concentrations of ozone and PAN (compare Section 1). Certain precautionary measures at the site can, however, reduce but not prevent the damaging effects of pollution. The measures available to reduce injury are questionable because they are only practical in agriculture and horticulture, limited in forestry, and not practical in natural ecosystems.

The possibilities of countering injurious pollutant effects in plant stands includes the use of genotypes possessing relative tolerance to the pollutant (4.3.2) and other modifying factors of plant response, such as external growth factors or various chemical protectants. The availability of differentially sensitive cultivars or individuals provides the possibility of breeding and growing relatively tolerant plant types. The influence of external environmental factors and chemicals to modify plant responses to photochemical oxidants leads to possible changes in cultivation practices, cultural requirements, and chemotherapeutic treatments to reduce photochemical oxidant injury to vegetation.

4.4.1 Differential Resistance as a Basis for Remedial Measures

Based on the considerable range in differential resistance, the cultivation of relatively tolerant species and cultivars provides the best available approach for reducing the impact of ambient oxidants. To be successful, however, detailed knowledge of the relative resistance relationships of the affected cultivars is needed. Also, the criteria used to determine the reduction in useful value (4.3.2.1) and the influence of internal (4.3) and external (4.2) growth factors on the plant response should be determined. An additional problem to consider is that the relative resistance relationships of individual plant species and types vary with different air pollutants, as has been observed with ozone and PAN (Hanson _et al_., 1976).

Cultural methods were used to moderate the injurious effects of photochemical oxidants on vegetation before the origin or the cause of the injury was known. The selection and culture of tobacco cultivars resistant to "weather fleck" injury preserved the cigar wrapper industry in the Connecticut River Valley from almost certain economic disaster. Subsequent studies showed that the selected cultivars had a significantly higher ozone tolerance than Bel-C which was no longer grown in the Connecticut River Valley because of its susceptibility to "weather fleck" injury (Menser and Heggestad, 1972). Additional studies confirmed a general relationship between plant resistance to "weather fleck" and ozone injury (Huang et al., 1975).

In the interim, numerous studies have illustrated the wide range in intraspecific susceptibility in agricultural and horticultural plant species as well as forest tree species (see Section 4.3.2). As expected, these results have and will continue to find practical use, particularly for sensitive cultivars or plant types in areas heavily impacted by photochemical oxidants. Knowledge of differentially sensitive species will obviously be used for the propagation of relatively resistant types (Jensen et al., 1976).

There is general agreement (Kress, 1976; Jensen et al., 1976; Bialobok et al., 1980) that the occurrence of autonomous resistance differences within a species provides the prerequisite conditions for breeding relatively tolerant plant types, particularly through positive selections and crossings. In conjunction with previous observations, the conditions are particularly favorable in some plant species for the artificial selection of differentially tolerant types. In onions (Allium cepa) for example, ozone resistance is controlled by a single dominant gene (Engle and

Gabelman, 1966). In Petunia hybrida, the genes responsible for oxidant tolerance act primarily in an additive manner with some indication of partial dominance in the progeny (Hanson et al., 1976). Partial dominance for both resistance and sensitivity has been reported for tobacco (Aycock, 1972; Provilaitis, 1967; Menser and Hodges, 1972; Huang et al., 1975). The data for corn indicate that the genes responsible for ozone sensitivity are either additive or incompletely dominant (Cameron, 1975). De Vos et al. (1980) studied the inheritance of peroxyacetyl nitrate resistance in Petunia hybrida Vilm. using inbreed parents of a suceptible F_1 hybrid and a resistant hybrid. In the experiment with the most severe PAN injury, genes for susceptibility exhibited almost complete dominance over those for resistance and epistatic effects were not significant. In other experiments with lower levels of PAN injury, resistance was partly dominant to susceptibility and one or more epistatic parameters were significant. The number of genes involved in photochemical oxidant tolerance in petunia, tobacco, and corn is not known but it is certainly greater than one. In contrast to previous observations in Phaseolus vulgaris (Saettler, 1975), crossing of two ozone sensitive and ozone resistant Phaseolus vulgaris cultivars found that ozone resistance was recessive and appeared to be regulated by a few major genes (Butler et al., 1979). Noteworthy in this connection, is a study of 387 snap bean cultivars grown in the United States in which approximately 70% were ozone tolerant (Meiners and Heggestad, 1979). Based on these observations, Meiners and Heggestad suggested that it was not necessary to breed bean cultivars specifically for resistance to oxidant air pollutants. However, breeding lines should be evaluated for sensitivity to photochemical oxidant air pollutants prior to being released to insure that susceptible types are not recommended or grown in areas impacted by photochemical oxidants. This recommendation is also true for other plant species.

Ozone or PAN concentrations above a specific level can exert a selection pressure, as do other environmental factors, in breeding experiments and in semi-natural and managed conditions. Accordingly, it appears reasonable to conclude that native plants will display a relative sensitivity level dependent on the natural ozone level. In the course of several decades, plants with a short generation cycle may develop resistant populations as a result of dynamic selection in areas experiencing increasing exposure from anthropogenic ozone and PAN (see the discussion in 2.5.2). Artificial selection studies conducted in areas experiencing elevated photochemical oxidant exposures should in the course of selections also attain a partial resistance to photochemical oxidant injury. Plant breeders generally attempt to select plants with the highest yield and the fewest injury symptoms, regardless of the cause.

Special breeding programs to develop ozone or PAN resistant cultivars are seldom described in the literature. However, examples include tobacco (Provilaitis and White, 1966; Huang _et_ _al_., 1975), loblolly pine (Heck and Brandt, 1977), petunia (Hanson _et_ _al_., 1974), and tomato (Clayberg, 1971, 1972). Given the intensive documentation of intraspecific differential sensitivity, findings about the nature of this resistance (see Chapters 2 and 4.3.2) and specific results (Huang _et_ _al_., 1975; Jensen _et_ _al_., 1976; Campbell _et_ _al_., 1977; Bialobok _et_ _al_., 1980), it is expected that breeding programs to enhance relative tolerance should be successful. From the perspective of agriculture, horticulture, and forestry, the increased breeding of plant types tolerant of photochemical oxidants is encouraged. However, from the broader perspective of environmental protection, such a course would be undesirable. The previous efforts to limit ambient concentrations of pollutants occurred primarily as a result of injury to economically important plant species. If economic losses are successfully reduced through extensive breeding and cultivating of tolerant types, it will lessen the urgency to decrease ambient concentrations, subsequently posing risks to natural vegetation and humans.

4.4.2 Fertilization, Irrigation, and Cultural Methods as Protective Measures

The reaction of plants to a given pollutant exposure fluctuates with the external growth factors. Therefore, this variation may be used to reduce the injurious effects of a pollutant exposure. However, a high probability of success should not be expected from these approaches.

Given the contradictory results from studies using various levels of individual plant nutrients (see 4.2.2.3), it is difficult to propose a general fertilization recommendation. However, in areas impacted by photochemical oxidants, a balanced fertilizer regime should be used. This regime would insure sufficient plant nutrients, so that during periods of low or no pollution the plants would be able to compensate for the pollution-induced injury. Several small applications of fertilizer are preferred because a single large application may increase plant sensitivity. Based on the observation of Heck and Dunning (1967), the elevation of the ambient CO_2 concentration in greenhouses should reduce the risk from photochemical oxidants. However, more information about the influence of CO_2 on pollutant uptake and pollutant effects is needed.

The proper supply of water to the plant is a decisive factor (4.2.1.4.1) in controlling pollutant uptake and therefore pollutant effects. In some areas particularly at risk from photochemical oxidants, tobacco farmers are warned by radio of predicted smog episodes and encouraged to reduce irrigation to the extent possible (Dean and Davis, 1972). However, the uncertainty of predicting smog episodes and the risk of reducing plant growth by decreasing the water supply when irrigation is decreased limits the usefulness of this preventive measure.

Experience with other air pollutants suggests that the control of the canopy structure by cultural measures could reduce photochemical oxidant effects. Isolated trees and shrubs, as well as plants on the edges of stands, experience a greater pollutant exposure. An early and extensive canopy closure can provide some protection through changes in air movement and by a filtering effect. The influx of polluted air is reduced in lightly thinned or compact canopies (Wentzel, 1963). In fruit culture, various training and pruning techniques should be used to develop a compact crown even though it may have some disadvantages. As a consequence of air pollution, shoot growth rate is reduced sooner than would be expected to occur from aging alone. Pruning as a means of regenerating both the vegetative and reproductive activity of trees or shrubs should be considered as well as the cultivation of locally adapted fruit types on vigorous root stocks (Guderian, 1969).

4.4.3 Protectants Against Photochemical Oxidants

Numerous chemicals are active in protecting plants and particular microorganisms from photochemical oxidants (Epstein and Bishop, 1977). The chemicals may be applied either as hydrates, aqueous solutions, emulsions, or powders that are either distributed on the plant surface, mixed with the soil, or injected to reduce injurious effects. Protective chemicals can be grouped as:

- antioxidants which may counteract the effects of photochemical oxidant air pollutants,
- biocides that are active against pathogenic fungi and animal pests, as well as photochemical oxidants,
- growth regulators that not only alter plant growth but also influence the sensitivity of plants to photochemical oxidants,
- various other chemical types that induce protection through diverse means.

4.4.3.1 Antioxidants

Antioxidants are compounds that prevent the reactions of organic compounds with molecular oxygen. These various chemical substances are used in numerous areas, for example protecting foods from discoloration and spoilage, as synergists in insecticides (Rubin et al., 1980), and in the formulation of rubber products as a protectants against ozone damage.

Any naturally available reductant such as ascorbic acid can act as a protectant (Barnes, 1972b). Ascorbic acid has been used in the Los Angeles area to reduce photochemical oxidant injury on numerous plant species such as beans, celery, romaine lettuce, petunias, and citrus (Freebairn and Taylor, 1960). For example, bean plants displayed only about 40% as much foliar injury when sprayed with K-ascorbate (0.01 N) as unsprayed controls. Studies with K- and Ca-ascorbate showed that the effectiveness of ascorbic acid depended on its uptake into the leaf (Freebairn, 1963). It is not known if the generally low protectant activity of ascorbic acid (Dass and Weaver, 1968) is attributed to the lack of any specific effect on O_3-

induced growth alternations, its autooxidation to dehydroascorbic acid (Siegel, 1962), or its limited uptake through the roots (Freebairn, 1963).

Of the numerous compounds developed as antioxicants, EDU N-[2-(2-oxo-1-imidazolidinyl) ethyl]-N'-phenylurea) is especially effective in protecting plants from ozone injury. For example, EDU reduced bronzing and delayed leaf drop in navy beans (Phaseolus vulgaris) more effectively than the systemic fungicides, carboxin, and benomyl (Hofstra _et_ _al_., 1978) or the antioxidants, piperonyl butoxide and n-propyl gallate (Rubin _et_ _al_., 1980). The protective effect of EDU, applied as either a foliar spray or soil drench, has been confirmed on petunia and chrysanthemum cultivars and numerous other herbaceous and woody species (Cathey and Heggestad, 1982a, b, c). Potato plants treated with either EDU or the fungicide chlorthalonil (tetrachloroisophthalonitrile) exhibited significantly less ozone and Alternaria solani blight injury than nonsprayed control plants. Furthermore, EDU was more effective (Bisessar, 1982). The combined effects of EDU and the fungicide, chlorthanlonil, were additive in reducing foliar ozone injury and increasing tuber weight.

The mechanism of antioxidant action may be to inhibit microsomal mixed function oxidases (m.f.o.) activity (Rubin _et_ _al_., 1980). This hypothesis may explain the protection offered by these types of compounds against injury. The m.f.o. system requires molecular oxygen for activity. Ozone is a "superactive" form of molecular oxygen; perhaps in plants treated with ozone the m.f.o. system becomes "superactive," abnormally oxygenating, peroxidating, or oxidating many different cellular constituents. Inhibiting the m.f.o. system with antioxidants could prevent this "superactivation" and thereby prevent ozone damage. An alternative hypothesis was proposed by Lee and Bennett (1982). Using EDU, they showed that it enhanced the activity of superoxidase dismutase (SOD) and catalase in bean leaves. They suggested that EDU enhanced the basic aerobic nature of the cells by inducing and regulating the oxidant-scavenging enzymes that protect the cells from oxyradicals formed during photosynthesis and where the plant experiences environmental stresses.

Gilbert et al. (1977) proposed that the protective mechanism of Santoflex 13 dust [N-(1,3-dimethylbutyl)-N'-phenyl-p-phenylene-diaminde] on apple seedlings, bean, melon, and tobacco plants, and also in the rubber industry resulted from its scavenging of ozone at the surface with the resultant formation of a surface film of ozonized antioxidant. The antioxidant diphenylamine (DPA) is an additional example of a chemical that reduced ozone injury (Elfving et al., 1976). A combined spray application of DPA and the antitranspirant "Wilt Pruf" on apple leaves was especially effective in diminishing visible and histological injury symptoms.

4.4.3.2 Biocides

The fungicides have attained the most significance of the various biocides used in agriculture, horticulture, and forestry for protecting plants from photochemical oxidant injury. The antioxidant properties of insecticides and herbicides have received little attention.

Studies during the 1950s showed that spray or dust applications of thiocarbamate fungicides, zineb (zinc ethylenebisdithiocarbamate), maneb (manganese ethylenebisdithiocarbamate), thiram (tetramethylthiuram disulfide), and ferbam (ferric dimethyldithiocarbamate) reduced the foliar injury of plants exposed to ozonated gasoline vapors or 1-hexane (Kendrick et al., 1954). In laboratory and the field studies, the degree of protection was directly related to the concentration of the chemicals (Kendrick et al., 1962). The protection was not systemic, but occurred only if the lower leaf surfaces were well covered, suggesting that the oxidants were deactivated at the surface through a reaction with the chemicals. Thiocarbamate did not reduce weather fleck injury on tobacco (Walker, 1967). Initially, plant protection studies focused on reducing ozone entry into the plant. However, present research methods use chemicals to alter the sensitivity of the plants at biochemical and physiological levels.

Systemic fungicides have received special attention, particularly those with antisenescence properties (Klingensmith, 1969). Numerous plant species, such as tobacco (Taylor, 1970; Reinert and Spurr, 1972), beans (Manning et al., 1973a, 1974; Pellissier et al., 1972a), grapevines (Kender et al., 1973), turf grasses (Moyer et al., 1974a; Papple and Ormrod, 1977), azaleas (Moyer et al., 1974b), and poinsettias (Manning et al., 1973b) are protected from ozone injury by applications of benomyl (methyl-1-butylcarbamoyl-2-benzimidazolecarbamate) as a spray, soil drench, or soil amendment. However, benomyl did not protect pinto beans from PAN injury (Pell, 1974; 1976). High concentrations (60 to 120 µg/g) of benomyl, incorporated into the soil increased the injurious effects of PAN on the leaves of "White Cascade" petunias (Pell and Gardner, 1979). It is possible that the antisenescence properties of benomyl maintained the plants at the optimal stage of sensitivity.

The antisenescence and antiozone properties of benomyl and related fungicide residues in the benzimidazole moiety (Pellissier et al., 1972b; Tomlinson and Rich, 1973). Ultrastructural studies of the palisade cells of pinto bean leaves found significant alterations in chloroplasts and other cellular structures, following an ozone exposure (0.25 ppm for 4 h), that did not occur in the benomyl treated plants (Rufner et al., 1975).

The chloroplast, plasmalemma, and tonoplast membranes were almost completely disrupted.

Other fungicides, including carboxin (5,6-dihydro-2-methyl-1,4-oxathiin-3-carboxanilide) and other 1,4-oxathiin derivatives (Rich et al., 1974; Curtis et al., 1975), thiophanate [diethyl 4,4'-o-phenyl-enebis (3-thioallophanate)] and its methyl and ethyl analogues (Moyer et al., 1974a; Seem et al., 1973), triarimol [α-(2,4-dichlorophenyl)-α-phenyl-5-pyrimidinemethanol] and EL 279 [α-(2-chlorophenyl)-α-cyclohexyl-5-pyrimidinemethanol] (Seem et al., 1972) also display some effectiveness against ozone injury.

Herbicides and insecticides can also influence plant response to ozone. Tobacco plants treated with chloramben (3-amino-2,5-dichlorobenzoic acid) lost their ozone tolerance (Carney et al., 1973) while isopropalin (2,6-dinitro-N,N-dipropylcumidine) protected greenhouse-grown flue-cured tobacco plants from ozone injury without significantly altering their leaf chemistry (Sung and Moore, 1979). In the field, tobacco plants treated with isopropalin or diphenamid (N,N-dimethyl-2,2-diphenylacetamide) reduced oxidant injury during the first 2 to 4 weeks following transplanting but not later in the season (Reilly and Moore, 1982). The finding that insecticides may interact with ozone is particularly important for integrated pest management programs (Teso et al., 1979). Lannate 90 SP (methomyl) and ozone interacted to produce a synergistic injury response, while treatment of bean leaves with Spectracide 25 EC (diazinon) significantly reduced ozone injury. Biocides may interact with themselves and ozone to influence plant response. For example, benomyl and carboxin counter the nematicide-induced stimulation of ozone injury to plants (Miller et al., 1976).

4.4.3.3 Growth Regulators

A series of studies have established that the phytohormones -- indoleacetic acid (IAA), gibberellic acid (GA), 6-benzylamine purine (BA), and abscisic acid (ABA) -- interact with photochemical oxidants (Hull *et al*., 1954; Ordin and Probst, 1962; Siegel, 1962; Runeckles and Resh, 1975b; Adedipe and Ormrod, 1972; Fletcher *et al*., 1974). The cytokinin, BA was more active in moderating the ozone-induced growth suppression and loss of chlorophyll in radish leaves than either IAA or GA (Adedipe and Ormrod, 1972). In contrast, an application of 6-furfurylaminopurine, a cytokinin similar to BA, increased the ozone susceptibility of tobacco plants (Lee, 1966). Foliar applications of benzimidazole, N-6-benzyladenine, and kinetin retarded the senescence of bean leaves, inhibited the loss of free sterols, and protected the plants against ozone injury (Tomlinson and Rich, 1973). The protection against ozone was achieved only when the chemical concentrations were sufficient to inhibit the degradation of chlorophyll. Compounds with antisenescent properties may retard the ozone-induced premature senescence (Walker, 1967; Pellisier *et al*., 1972b; Seem *et al*., 1972). The observed protection induced by these chemicals was not, in general, great enough that these compounds will attain significant practical use as protectants against photochemical oxidants. However, individual phytohormones are well suited for investigating some of the detailed questions concerning the mode of ozone action in plants (Runeckles and Resh, 1975b; Tomlinson and Rich, 1973).

Growth retardants are effective in reducing ozone injury on plants. For example, CBBP (2,4-dichlorobenzyltributyl phosphonium chloride) and SADH (succinic acid 2,2-dimethyl hydrazide) reduced ozone injury on petunias (Cathey and Heggestad, 1972). However, to be effective, the SADH concentration had to be at least twice the concentration used to retard stem elongation. Adding L-ascorbic acid and a wax coating to the spray solution increased the protection afforded by SADH. Chemicals that did not retard petunia growth, for example chloromequat [(2-chloroethyl] trimethyl ammoniumchloride) and ancymidol [α-cyclopropyl-α(4-methoxyphenyl)-5-pyrimidine methanol] failed to protect plants against ozone. Applications of ancymidol and chlomequat reduced ozone and sulfur dioxide induced foliar injury in eight poinsettia cultivars (Cathey and Heggestad, 1973). Increased air pollution tolerance was believed to be partly the result of a series of morphological changes and also reduced penetration of O_3 and SO_2 into the susceptible tissues.

4.4.3.4 Other Chemicals

On the leaf surface, various chemicals protect plants against ozone injury. Folicote (an emulsion of paraffinic hydrocarbon waxes), an antitranspirant, provided good protection against ozone injury in four genera of the Solanaceaes family (Knapp and Fieldhouse, 1970) and beans (Pellisier *et al*., 1972a, c). Spray coverage of both leaf surfaces was required to obtain complete protection. The Folicote treatment presumably reduced ozone uptake into the leaf and therefore foliar injury was reduced.

Dusts of various particulate substances -- charcoal, diatomaceous, ferric oxide -- reduced ozone injury on tobacco plants (Jones, 1963). These various compounds apparently cause a catalytic destruction of ozone at the leaf surface.

4.4.3.5 Summary of the Practicality of Chemical Protectants

Even though examples were given to confirm that various chemicals can reduce ozone injury, this should not lead to the conclusion that they are practical for preventing ozone and PAN-induced injury. Regardless of the activity of a particular chemical, practical conditions limit their use:

- The protective action depends on the chemical (Ormrod, 1978), its time of application (Curtis _et al_., 1975; Papple and Ormrod, 1977), plant species and cultivars (Manning _et al_., 1974), as well as their developmental stage (Pell, 1974; 1976). Also, the chemical has a limited period of effectiveness (Manning _et al_., 1973a, b; Miller _et al_., 1976).
- The compound must be applied from a few to many times during the plant growth period, because the effective period of the chemical is limited (Kender _et al_., 1973). In this case, the price of the particular chemical and its cost of application limit its possible uses, especially if these chemicals do not also function as biocides in plant cultivation practices.
- Because of price, the application of protectants is frequently only possible during smog episodes. However, there is a large uncertainty associated with predicting smog events.
- The protectants are not equally effective for all air pollutants. Benomyl, for example, can prevent ozone injury (see 4.4.3.2) but not injury from other oxidants (Pell and Gardner, 1979).
- Finally, the use of protectants is limited because they may have other toxic effects or lead to the formation of compounds, in food and fodder plants, that are toxic to animals and humans

(Manning _et al_., 1973a; Klingaman and Link, 1975; Papple and Ormrod, 1977).

CHAPTER 5
EFFECTS OF POLLUTANT COMBINATIONS

Photochemical oxidants are a widely distributed, complex array of compounds that may co-occur on either a local or regional scale with other pollutants emitted from various sources. Consequently, plants grown in the natural environment are seldom exposed to single pollutants but rather to varying combinations and concentrations of several atmospheric components. Thus, when assessing the responses of plants in the field, the effects of pollutant combinations should be considered in addition to the impacts of individual pollutants.

5.1 Pollutant Combinations

There are several reviews of the effects of pollutant combinations on vegetation (e.g., Reinert et al., 1975; Ormrod, 1982). Preceding the publication of Menser and Heggestad (1966) information on the effects of pollutant mixtures was limited. However, their report provided the initial impetus for extensive research on this topic. They showed that Bel W-3 tobacco plants exposed to ozone (0.03 ppm) or sulfur dioxide (0.24-0.28 ppm) were uninjured but that substantial foliar injury occurred when the plants were exposed to both gases simultaneously. The authors called this response a synergistic effect. Subsequent studies confirmed this finding and extended the observations to show that pollutant combinations can influence not only foliar injury responses but numerous other plant processes. These plant responses to pollutant combinations depend not only on the components of the mixtures but also the concentrations of the individual pollutants, their temporal succession, and may be modified by external and internal growth factors.

This chapter will focus on the effects of ozone in combination with other pollutants and the factors that modify the response. The majority of the published research has discussed ozone-sulfur dioxide combinations; studies concerning the effects of ozone with other pollutants.are limited. In describing the effects of pollutant combinations, the authors will follow the same logical approach as used for discussing ozone and PAN in the other chapters -- mode of action, diagnosis, and factors influencing plant response.

In describing the effects of pollutant combinations, a number of terms have attained general, though not universal, acceptance to illustrate the range of responses that may occur with the simultaneous or alternating occurrence of two or more pollutants. The following concepts were not derived from an understanding of the toxicology of the mixtures but rather from a cursory review of statistical terms:

-- The plant response to the two pollutants is independent (no interaction). The response to pollutant A is not altered by a concurrent exposure to pollutant B.

-- The plant response to the pollutant mixtures is additive. The response to the mixture is similar to the summed effects of the individual pollutants.

-- The plant response may be less than additive (antagonistic). The response to the pollutant combination is less than the summed response to the individual pollutants.

-- The plant response may be greater than additive (synergistic). The response to the pollutant combination is greater than the summed effects of the individual pollutants.

5.2 Ozone and Sulfur Dioxide

5.2.1 Mode of Action

Both ozone and sulfur dioxide influence various biochemical and physiological processes with many of their responses associated with changes in membrane permeability. Low concentrations of ozone and sulfur dioxide induce similar stress symptoms, including premature senescence. Slightly higher concentrations can affect individual metabolic processes. The primary biochemical responses of ozone are based on its high oxidation potential and its tendency to form free radicals; SO_2 can also form free radicals but it may also be a weak oxidant (Puckett _et_ _al_., 1973), a weak acid, or as sulfite (or sulfate) perturb relations and enzyme regulation (Ziegler, 1973). Because the mode of action of the individual pollutants is not well understood, it is difficult to predict the mode of action of pollutant combinations. This situation is confounded by the limited research in this area. However, plant response to pollutant mixtures is controlled by the same general processes that control response to ozone: the amounts of pollutants that diffuse into the plant, the rate of scavenging reactions that reduce cellular concentrations protecting reactive sites, and the rate and amount of homeostatic processes (Chapter 2; also see Figure 2).

5.2.1.1 Pollutant Uptake

The importance of stomatal control and pollutant uptake in multiple pollutant studies became apparent from earlier work on the uptake of single gases and the observations that pollutants that did not enter the plant were generally not phytotoxic. The implied hypothesis has been that the pollutant combinations interfered with normal stomatal mechanisms allowing greater pollutant uptake than for the individual pollutants.

Leaf resistance data were compared for species that responded synergistically to the combination of ozone plus sulfur dioxide (radish, cucumber) and species that did not (soybean, white bean) (Beckerson and Hofstra, 1979a, b). For both groups, leaf resistance tended to decrease following exposure to sulfur dioxide and increase following exposure to ozone; the two pollutants combined caused a greater increase in leaf resistance than ozone alone. The stomata of ozone-sensitive petunia cultivars closed more rapidly in the presence of ozone and sulfur dioxide mixtures, while the stomata of ozone-insensitive cultivars closed more slowly (Elkiey and Ormrod, 1979c). However, neither the synergistic nor antagonistic response could be explained by the changes in stomatal behavior. Peas reacted synergistically to ozone-sulfur dioxide mixtures, but neither the amount of injury nor the synergistic response was associated with stomatal resistance (Olszyk and Tibbitts, 1981).

The uptake of ozone and sulfur dioxide singly and in combination was studied in three petunia cultivars that differed in sensitivity to the pollutants (Elkiey and Ormrod, 1980a, 1981a). Pollutant uptake for the single gases and the mixtures was generally greater for the more sensitive petunia cultivars. The uptake of ozone and sulfur dioxide was greater from single gas exposures than for the uptake of the same gases from the mixtures (Elkiey and Ormrod, 1981a). Uptake rates decreased throughout the day and from day to day, but the reduction was larger for the combinations than from the single gases. Similar results were found with *Poa pratensis* cultivars that differed in pollutant sensitivity (Elkiey and Ormrod, 1981b).

Studies of the sulfate content of petunia tissues following exposure to SO_2 with and without ozone confirmed the previous reports of stomatal behavior and gas uptake (Elkiey and Ormrod, 1981c). At 90% relative humidity, the plants contained less sulfate after being exposured to a mixture of SO_2 plus ozone than from SO_2 alone. Similar trends were observed in the older leaves when the plants were exposed at 50% relative humidity.

Data from studies of stomatal behavior, pollutant uptake, and tissue sulfate content all confirm that the uptake of individual gases from pollutant mixtures is less than the uptake rates of the individual gases alone. However, this trend should not be interpreted as a contradiction in relation to the possible synergistic effects of pollutant combinations. Even though the uptake of individual gases from mixtures is less, the total number of molecules of absorbed pollutants is greater from mixtures; this probably contributes to their greater phytotoxicity.

5.2.1.2 Perturbation

The modes of action for ozone and sulfur dioxide, individually, are not well understood or documented; the modes of action for pollutant combinations are even more obscure. The few relevant studies have focused on changes in membrane permeability because the primary site of ozone is thought to be plant membranes. Three petunia cultivars that varied in their ozone sensitivity were used to study the effects of ozone and sulfur dioxide, singly and in combination, on potassium and total electrolyte leakage as indicators of membrane permeability (Elkiey and Ormrod, 1979d). Potassium efflux was not increased by a 5-h exposure but total electrolytes were elevated in the intermediate and sensitive petunia cultivars exposed to ozone. Sulfur dioxide had no significant effect while the pollutant combination increased the electrolyte leakage of all three cultivars. The effects of the pollutants individually and in combination on the leaf water potential of the three cultivars were also studied (Elkiey and Ormrod, 1979a). Ozone rapidly decreased the leaf water potential. The decline was largest in the cultivar intermediately sensitive to ozone; sulfur dioxide had no significant effect. In contrast, the pollutant mixture caused a smaller decrease and the rate of decline was less rapid than for ozone alone.

Beckerson and Hofstra (1980) studied the effects of pollutant combinations on membrane permeability, as measured by electrolyte leakage, in several species that showed either an "antagonistic" or "synergistic" injury response to the combinations. Ozone significantly increased electrolyte leakage from soybean and white bean (species that displayed an antagonistic foliar injury response) prior to visible injury. However, the mixture did not stimulate electrolyte leakage. Sulfur dioxide apparently moderated the ozone effects on the membrane. Ozone had no significant effect on electrolyte leakage from either radish or cucumber (species that displayed a synergistic foliar injury response) but the combination of ozone and sulfur dioxide significantly increased leakage.

Changes in membrane permeability as determined by changes in electrolyte leakage or leaf water potential do not show definite patterns. This may mean that potassium or total electrolytes were not the best indicators of membrane impacts or that the plasma membrane is not the membrane system most sensitive to pollutant combinations.

5.2.1.3 Injury

Physiological and biochemical changes induced by mixtures of ozone and sulfur dioxide have been only sparingly studied. The reduction of net photosynthesis in alfalfa (Medicago sativa) exposed to ozone and SO_2 or ozone and NO_2 was additive when compared to the reductions induced by the individual pollutants (Bennett and Hill, 1974). In contrast, the reduction in net photosynthesis for sugar maple and white ash was more than additive after two days of exposure (Carlson, 1979). The net photosynthesis of Vicia faba was reduced when the ozone concentration exceeded 0.05 ppm for 4 h but, unless visual injury developed, it returned to the control level following the fumigation (Black et al., 1982). The addition of 0.04 ppm SO_2 caused a significantly greater reduction in photosynthesis than ozone alone. The SO_2 had the effect of reducing the ozone concentration that was inhibitory to photosynthesis. The addition of SO_2 had no effect on the photosynthetic recovery rate. In studies with sunflower, neither O_3 nor SO_2 inhibited photosynthesis but mixtures of the gases at the same concentrations as used previously significantly reduced photosynthesis (Furukawa and Totsuka, 1979).

In white bean, which displayed an antagonistic response to $O_3 + SO_2$ mixtures, the chlorophyll content was reduced by exposure to the mixture but the reduction was detected two days later than it was observed in exposures to ozone alone (Beckerson and Hofstra, 1979c). However, after five days the chlorophyll loss was greater in the pollutant combination than from the individual pollutants. The pollutant combination had no significant effects on protein or RNA levels. The carbohydrate and protein contents of Ulmus americana leaves were reduced within 24 h following exposure to mixtures of $O_3 + SO_2$ but within 4 weeks after exposure the concentrations were comparable to control leaves (Constantinidou and Kozlowski, 1979a).

Poplar leaves exposed to O_3 and SO_2 singly and in combination showed no visible foliar symptoms (Krause and Jensen, 1978). However, scanning electron micrograph studies showed crystalline-like inclusions in the bundle-sheath extension cells exposed to the combination. Globules were observed in mesophyll cells and the chloroplasts appeared distorted and damaged only from the mixture. Scanning electron micrograph studies of poplar leaf surfaces showed that pollutant combinations induced changes that were not detected following exposure to the single gases (Krause and Jensen, 1979).

5.2.2 Effect on Plants

In addition to metabolic studies, numerous other reports have documented the effects of mixtures of O_3 and SO_2 on visible injury and plant growth and yield. As in the metabolic studies, these effects have shown responses ranging from antagonistic to synergistic.

5.2.2.1 Foliar Injury

The types of responses and the magnitudes of effects of pollutant exposures on visible injury are shown for selected species in Table 14. Brief exposures of tobacco Bel W-3 to mixtures of SO_2 (0.24-0.28 ppm) and ozone (0.03 ppm) produced visible injury while exposure to the individual pollutants did not (Menser and Heggestad, 1966). In a series of experiments, Tingey et al. (1973d) studied the effects of brief exposures of ozone and SO_2 on 11 different plant species. Tobacco, radish, and alfalfa exhibited a greater than additive response; with cabbage, broccoli, and tomato, the injury was additive or less. The concentrations used in these studies and others (Reinert et al., 1970; Jacobson and Colavito, 1976) were in the same range as measured ambient concentrations of combined pollutants. Begonias exposed to low concentrations of the combined gases for 5 days exhibited a synergistic response for visible injury (Gardner and Ormrod, 1976). Studies with peas (Olszyk and Tibbitts, 1982) showed that the concentration and duration of exposure to the mixture had to be significantly reduced to maintain a similar degree of injury as that induced by the individual pollutants. However, in soybean and white bean the injury intensity caused by the mixture was reduced and the rate of symptom development delayed compared to effects caused by ozone alone (Hofstra and Ormrod, 1977).

The chlorotic dwarf syndrome of eastern white pine (see 3.1.1) was produced by chronic exposures to SO_2 and O_3 singly or in combination (Dochinger et al., 1970). Following an 8-week exposure to intermittent concentrations of O_3 and SO_2 (each at 0.10 ppm), a sensitive clone of eastern white pine displayed 16% needle necrosis. Exposures to the individual pollutants caused only 3 to 4% needle injury (Dochinger et al., 1970). Eastern white pine clones from visibly injured mother trees from pollution-impacted areas displayed a greater than additive amount of injury, measured as longitudinal growth, following exposure to a mixture of ozone (0.025 ppm) and sulfur dioxide (0.05 ppm) (Houston, 1974). A SO_2-sensitive clone of eastern white pine exposed to O_3 (0.05 ppm for 2 h) developed no visible injury, exposure to SO_2 (0.05, 2 h) caused a moderate amount of injury, exposure to the mixture (each at 0.05 ppm) caused less injury. Sequential exposures to O_3 and SO_2 for 2 hours each followed by an exposure to the combined pollutants 24 hours later caused the most injury

Table 14. Visual Injury on Various Plants Induced by the Joint Action of Ozone and Sulfur Dioxide

Plant Species	Concentration ppm		Exposure Duration	Effect		Literature
	O_3	SO_2		Intensity	Type[1]	
Tobacco (Nicotiana tabacum)						
-- Bel W_3	0.03	0.24	2 h	15%	+	Menser and Heggestad, 1966
	0.03	0.28	4 h	41%	+	
-- Bel-B	0.03	0.24	2 h	9%	+	Menser and Heggestad, 1966
	0.03	0.28	4 h	23%	+	
-- Bel-B	0.05	0.25	4 h	4%	+	Tingey et al., 1973d
	0.1	1.0		34%	+	
-- Bel W_3	0.05	0.25	4 h	17%	+	
	0.1	1.0		48%	+	
	0.05	0.5		60%	+	
	0.1	0.1		95%	0	
	0.1	0.25		85%	+	
	0.1	0.5		96%	+	
Tobacco (Nicotiana glucinosa)	0.03	0.45	2/4 h	26/39%	+/+	Grosso et al., 1971
Tobacco (Nicotiana rustica va. brasilia)	0.03	0.34	2/4 h	35/33%	+/+	Grosso et al., 1971
Bean (Phaseolus vulgaris)	0.19	1.7	0.8 h	24%	+	Matsushima, 1971
	0.37	1.6	1.0 h	24%	*	
Lima Bean (Phaseolus limensis)	0.05	0.25	4 h	0%	*	Tingey et al., 1973d
	0.1	1.0		9%	*	
Soybean (Glycine max)	0.3	1.0	6h	13-38%	*	Reinert et al., 1975

(continued)

Table 14 (continued)

Plant Species	Concentration ppm		Exposure Duration	Effect		Literature
	O_3	SO_2		Intensity	Type[1]	
Soybean (Glycine max)	0.15	0.15	6 h/day 5 days	1%	-	Hofstra and Ormrod, 1977
	0.15	0.30		0%	-	
Soybean (Glycine max)	0.5	0.25	4 h	0%	*	Tingey et al., 1973d
	0.1	1.0		1%	*	
White Bean (Phaseolus vulgaris)	0.15	0.15	6 h/day 5 days	1%	-	Hofstra and Ormrod, 1977
	0.15	0.30		0%	-	
Pea (Pisum sativum)	0.11	0.11	4 h	6%	+	Olszyk and Tibbitts, 1982
Broccoli (Brassica oleracea L. var. botrytis)	0.05	0.25	4 h	3%	*	Tingey et al., 1973d
	0.05	0.5		17%	+	
	0.1	0.1		34%	+	
	0.1	0.25		11%	0	
	0.1	0.5		19%	0	
	0.1	1.0		32%	+	
Cabbage (Brassica oleracea) var. capitata)	0.05	0.25	4 h	0%	*	Tingey et al., 1973d
	0.05	0.5		4%	*	
	0.1	0.1		22%	0	
	0.1	0.25		14%	0	
	0.1	0.5		54%	+	
	0.1	1.0		28%	0	
Alfalfa (Medicago sativa)	0.05	0.25	4 h	0%	*	Tingey et al., 1973d
	0.05	0.5		2%	*	
	0.1	0.1		24%	+	
	0.1	0.25		21%	+	
	0.1	0.5		60%	+	
	0.1	1.0		3%	*	

(continued)

Table 14 (continued)

Plant Species	Concentration ppm		Exposure Duration	Effect		Literature
	O_3	SO_2		Intensity	Type[1]	
Radish (Raphanus sativus)	0.05	0.25	4 h	7%	*	Tingey et al., 1973d
	0.05	0.4		7%	*	
	0.1	0.1		50%	+	
	0.1	0.25		22%	+	
	0.1	0.5		46%	+	
	0.1	1.0		45%	0	
Tomato (Lycopersidon esculentum)	0.05	0.25	4 h	3%	*	Tingey et al., 1973d
	0.05	0.5		1%	*	
	0.1	0.1		50%	-	
	0.1	0.25		10%	0	
	0.1	0.5		13%	0	
	0.1	1.0		2%	*	
Spinach (Spinacia oleracea)	0.05	0.25	4 h	0%	*	Tingey et al., 1973d
	0.1	1.0		1%	*	
Onion (Allium cepa)	0.5	0.25	4 h	0%	*	Tingey et al., 1973d
	0.1	1.0		3%	*	
Bromegrass (Bromus inermis)	0.05	0.25	4 h	0%	*	Tingey et al., 1973d
	0.1	1.0		4%	*	
Begonia (Begonia sp.)	0.3	1.2	1 d	43%	+	Gardner and Ormrod, 1976
Grape (Vitis labuscana)	0.4	0.4	4 h	47%	+	Shertz et al., 1980a
	0.8	0.8	4 h	84%	-	
Eastern White Pine (Pinus strobus)	0.10	0.10	8 h/day for 8 week	16%	+	Dochinger et al., 1970

(continued)

Table 14 (continued)

Plant Species	Concentration ppm		Exposure Duration	Effect		Literature
	O_3	SO_2		Intensity	Type[1]	
Eastern White Pine (Pinus strobus)	0.05	0.05	2 h	6.5 (Index 1 to 7)	-	Costonis, 1973
Eastern White Pine (Pinus strobus)	0.025	0.05	6 h	16%	+	Houston, 1974
Trembling Aspen (Populus tremuloides)	0.05	0.20	3 h	11%[2]	+	Karnosky, 1976
	0.05	0.20	38	17%	+	

[1] Type of response.
+ = Greater than additive;
0 = additive;
- = less than additive;
* = not determined or not significant.

[2] Injury expressed as percentage of leaves injured/plant.

(Costonis, 1973). Scotch pine exposed to the combined pollutants displayed less injury than plants exposed to SO_2 alone; O_3 did not induce foliar injury (Nielsen et al., 1977).

5.2.2.2 Growth Effects

In addition to the mixture effects on physiological processes and foliar injury, most recent studies have focused on the mixture effects on plant growth and yield. Growth and yield studies have been conducted in both greenhouse and field exposure chambers. Most of the studies used O_3 but there have been a few reports of the interaction between ambient photochemical oxidants and SO_2. Selected examples of the effects of O_3 and SO_2 mixtures on the growth of various plant species are shown in Table 15.

Mixtures of O_3 (0.05 ppm) and SO_2 (0.05 ppm) for 8 h/day, 5 days/week for 5 weeks reduced the growth and yield of radishes (Tingey et al., 1971). The pollutant mixture caused a greater than additive reduction in shoot growth and a less than additive reduction in root growth. In other studies using the same pollutant concentrations, growth reductions for tobacco Bel-W3 (Reinert et al., 1969), soybean (Tingey et al., 1973b), and alfalfa (Tingey and Reinert, 1975) were generally additive. Field studies with alfalfa (Neely et al., 1977) showed that exposure to mixtures of O_3 (0.05 ppm, 7 h/day) and SO_2 (0.05 ppm, 24 h/day) for 68 days reduced shoot, stubble, and root dry weights to a similar extent as those caused by either pollutant alone. Alterations were also observed in various metabolites. Growth reductions in soybeans exposed to O_3 (0.10 ppm) and/or SO_2 (0.10 ppm) for 6 h/day throughout the growing season in field exposure chambers were approximately additive (Heagle et al., 1974). Additional studies with soybeans (Heagle et al., 1983), in which the plants were exposed to O_3

Table 15. The Effect of the Joint Action of Ozone and Sulfur Dioxide on Plant Growth

Plant Species	Concentration ppm		Exposure Duration	Effect		Literature
	O_3	SO_2		Growth[1] Reduction	Type[2]	
Tobacco (Nicotiana tabacum) Bel-W_3	0.05	0.25	8 h/d; 5 d/w; 4 w	32% SDW 49% RDW	0 +	Tingey and Reinert, 1975
Soybean (Glycine max)	0.1	0.1	6 h/d; 43 d	53% SFW	0	Heagle et al., 1974
			92 d	53% SFW	0	
			133 d	73% SFW	0	
				51% pod number	0	
				66% seed weight/plant	0	
Soybean (Glycine max)	0.25	0.25	4 h/d; 3 d/w; 11 w	64% PDW	0	Reinert and Weber, 1980
Alfalfa (Medicago sativa)	0.05	0.05	8 h/d; 5 d/w; 12 w	18% SDW 24% RDW	- -	Tingey and Reinert, 1975
Radish (Raphanus sativus)	0.45	0.45	4 h	16% SDW[3] 70% RDW	0	Tingey and Reinert, 1975
	0.05	0.05	8 h/d; 5 d/w; 5 w	10% SDW 55% RDW	0	Tingey et al., 1971
Begonia (Begonia sp.) Early vegetative stage	0.15	0.6	5 d	8% SDW[4]	*	Gardner and Ormrod, 1976
	0.15 0.3	0.6 1.2	5 d succes- 1 d sively	40% SDW	+	
	0.15	0.6	5 h	5% SDW[3]	*	
	0.15 0.3	0.6 1.2	5 d succes- 1 d sively	23% SDW	+	

(continued)

Table 15 (continued)

Plant Species	Concentration ppm		Exposure Duration	Effect		Literature
	O_3	SO_2		Growth[1] Reduction	Type[2]	
Prefloral stage	0.15	0.6	5 d	11% SDW[4]	*	
	0.15 0.3	0.6 1.2	5 d succes- 1 d sively	8% SDW	*	
	0.15	0.6	5 d	10% SDW[5]	*	
	0.15 0.3	0.6 1.2	5 d succes- 1 d sively	10% SDW	*	
Kentucky bluegrass (Poa pratensis)	0.15 (+ 0.15 ppm NO_2)	0.15	10 d (ozone: 6 h/d; 10 d)	1-50% leaf area	0	Elkiey and Ormrod, 1980b
Red top (Agrostis alba)				28% leaf area	0	
Creeping bentgrass (Abrostis palustris)				26% leaf 1431	0	
Colonial bentgrass				90/70% leaf area	+/0	
Red fescue (Festuca rubra)				90/70% leaf area	+/0	
Perennial ryegrass (Lolium perenne)				13% leaf area	0	

(continued)

Table 15 (continued)

Plant Species	Concentration ppm		Exposure Duration	Effect		Literature
	O_3	SO_2		Growth[1] Reduction	Type[2]	
Eastern White Pine (Pinus strobus)	0.025	0.5	6 h			
-- Sensitive clone				52% needle length	-	Houston, 1974
-- Tolerant clone				32% needle length	-	
Scotch pine (Pinus silvestris), 17 clones	2.0	1.0	6 h/d; 4 d	4-39% shoot height	-	Bialobok et al., 1980
Yellow poplar (Liriodendron tulipfera)	0.1	0.1	12 h/d, 7 d/w, 50 days	7%[6]	-	Jensen, 1981b
Cottonwood (Populus deltoides)	0.1	0.1	12 h/d, 7 d/w, 50 days	55%[6]	-	Jensen, 1981b
Hybrid Poplar (Populus deltoides x P. trichocarpa)	0.25	0.50	12 h/d, 24 d	59% PDW	-	Noble and Jensen, 1980
Poplar (Populus x euramericana)	0.035	0.06	SO_2, 24 h/d O_3, 12 h/d, for 28 days	12-25% PDW	0/+	Mooi, 1981
Poplar (Populus maximowiczii)	0.035	0.06	SO_2, 24 h/d, O_3, 12 h/d, for 28 days	15-27% PDW	0/+	Mooi, 1981

(continued)

Table 15 (continued)

Plant Species	Concentration ppm		Exposure Duration	Effect		Literature
	O_3	SO_2		Growth[1] Reduction	Type[2]	
Apple (Malus domestica)	0.4	0.4	4 h	45% shoot growth	+	Shertz *et al.*, 1980b

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[1] SFW = shoot fresh weight.
SDW = shoot dry weight.
RDW = root dry weight.
PDW = plant dry weight.

[2] Type of response:

[3] 11 days following exposure.

[4] 2 weeks following exposure.

[5] 8 weeks following exposure.

[6] Relative growth rate.

(0.025 to 0.125 ppm, 7 h seasonal mean for 111 days) and SO_2 (0.0 to 0.367 ppm, 4 h seasonal mean for 101 days) indicated that the resultant growth reductions were the consequence of the independent action of the two gases. The shoot fresh weight of white beans exposed to the combination of O_3 (0.15 ppm) and SO_2 (0.15 ppm) for 5 or 10 days was reduced less by the combination than by O_3 acting alone (Hofstra and Ormrod, 1977). Mixtures of O_3 and SO_2 had a greater impact on radish hypocotyl than foliage growth; when low concentrations of NO_2 were added into the mixture it tended to intensify the yield reduction even though NO_2 alone did not decrease growth (Reinert and Gray, 1981; Reinert et al., 1982).

In contrast to herbaceous plants which tended to display additive or synergistic growth responses, the majority of the studies on woody vegetation have shown less than additive or antagonistic responses on plant growth from the pollutant mixtures. Although the combination of O_3 and SO_2 caused significant growth reductions in cottonwood, yellow poplar, and hybrid poplar, the reductions were less than expected from the responses of the individual gases (Jensen, 1981b; Noble and Jensen, 1980). Even in white pine where the chlorotic dwarf syndrome has been associated with exposures from pollutant mixtures, growth effects tended to be less than additive (Houston, 1974). One week following a single exposure to SO_2 or O_3 singly or in combination, Ulmus americana leaf expansion was reduced by both the sulfur dioxide and combination treatments (Constantinidou and Kozlowski, 1979b). However, within two weeks the growth rates in those treatments had returned to the control rate, indicating that the plants had recovered, but the final leaf area was still reduced. In hybrid poplar cuttings exposed to chronic levels of O_3 and SO_2 in combination and individually, growth analysis indicated that the growth rate and net assimilation rate displayed a synergistic reduction when compared to the effects of the individual pollutants (Jensen, 1981c). In poplars, chronic exposures to pollutant mixtures stimulated leaf abscission (Noble and Jensen, 1980; Mooi, 1981). The enhanced leaf drop may, in part, be associated with the observed growth reduction.

Interactive effects were also observed when SO_2 was added to ambient photochemical oxidants. Oshima (1978) found that the addition of SO_2 to ambient oxidant caused a significant reduction in kidney bean yield and plant biomass even though the same oxidant dose without SO_2 caused no significant reduction. The yield of snap beans displayed a significantly greater reduction when SO_2 was added to the chambers than from ambient oxidant alone (Heggestad and Bennett, 1981). However, the authors indicated that the SO_2 concentration was unusually high and would not represent ambient conditions. The yield of potatoes was similarly reduced from ambient oxidant, with or without added SO_2. However, the combination treatment significantly altered the nitrogen content of the tubers (Foster et al., 1983).

At concentrations of 0.05 or 0.10 ppm for O_3 and SO_2, the foliar injury response tended to be synergistic or at least additive. Chronic exposures to mixtures of O_3 + SO_2 reduced the growth of woody and herbaceous plants to varying amounts. Although the mixtures caused significant growth reductions, the effects on woody plants tended to be less than additive, while the effects on herbaceous plants ranged from less than additive to additive (i.e., the effects of the combination could be estimated from the effects of the individual gases). In practice, yield reductions have been observed in the concentration range of 0.05 ppm ozone (0.10 mg m^{-3}) and 0.05 ppm sulfur dioxide (0.14 mg m^{-3}). In determining the environmental significance of exposures to pollutant mixtures, special consideration must be given to the concentrations and durations of exposures. The exposure conditions used in some studies may provide useful scientific information but they deviate significantly from ambient exposure conditions restricting the usefulness of the data for direct evaluation of environmental problems.

5.2.3 Diagnosis of Effects

The factors to considered when attempting to diagnose a probable cause of injury were discussed in Chapter 3 as were detailed descriptions of ozone and PAN injury. The initial report of O_3-SO_2 synergism on tobacco described the injury from the mixture as tiny white flecks scattered randomly over the upper leaf surface and stated that the symptoms resembled O_3 injury (Menser and Heggestad, 1966). In other species, the injury was characterized as stipple or small discrete interveinal necrotic and/or clorotic lesions on the upper leaf surface (Tingey _et_ _al_., 1973d). An intense red pigmentation, stippling, and silvering of the interveinal areas were observed on the lower leaf surface. The similarity between the symptoms induced by O_3 or the mixture of O_3 and SO_2 have been observed in numerous species (e.g., Tingey _et_ _al_., 1973d; Olszyk and Tibbitts, 1982; Reinert and Nelson, 1980). In beans, the symptoms ranged between tan interveinal necrosis associated with bifacial injury to silvering of the lower leaf surface, depending on temperature (Miller and Davis, 1981). However, in white bean O_3 induced a bronze flecking on mature leaves while SO_2 caused a bifacial necrosis (Hofstra and Ormrod, 1977). In contrast, the symptoms of the combined gases appeared as a yellow interveinal chlorosis becoming apparent several days later than the ozone symptom would. In soybean, characteristic ozone injury appeared following exposure to the combined gases but the symptoms appeared several days later than on plants exposed to ozone alone (Hofstra and Ormrod, 1977). The undersurface of newly-developed petunia leaves became glazed after exposure to a combination of O_3 and SO_2, which was similar to the description of PAN injury (Lewis and Brennan, 1978). The injury followed a similar distribution with leaf development as PAN. In trembling aspen, the foliar symptoms caused by the two-pollutant combination were similar to those induced by the individual pollutants (Karnosky, 1976). The foliar symptoms of chlorotic dwarf of white pine were similar whether induced by ozone or the mixture of ozone and sulfur dioxide (Dochinger et al., 1970).

The general similarity between the symptoms induced by ozone and the mixture of ozone and sulfur dioxide may explain why foliar injury may occur without the occurrence of elevated ozone concentrations. This similarity may also complicate the field diagnosis and make it difficult to assign the cause to a specific pollutant based on visible injury alone.

5.2.4 Factors Influencing Plant Response

Various external and internal growth factors would be expected to influence the magnitude and possibly the type of plant response to pollutant mixtures, just as they do for the individual pollutants. There have been only a few studies concerning the influence of plant or environmental factors as they influence plant response to pollutant mixtures. However, it is anticipated that developmental or environmental factors that alter pollutant uptake, pollutant scavenging, or homeostatic processes would also be expected to influence the response to pollutant combinations.

5.2.4.1 Concentration and Duration

The magnitude of plant responses to pollutant combinations tends to increase with increasing concentration of each gas, as is true when the gases are applied individually. However, the type of response is not consistent with concentration. Menser and Heggestad (1966) observed foliar injury on tobacco below the injury threshold of each gas. In contrast, MacDowall and Cole (1971) found the synergistic response below the injury threshold for SO_2 but not below the O_3 injury threshold. Synergism was most pronounced at the injury threshold doses for each pollutant. Jacobson and Colavito (1976) showed that the extent of synergistic or antagonistic responses in tobacco and bean plants depended not only on the species but also the concentrations of each gas. Studies with soybean (Heagle and Johnston, 1979) showed plants could display both synergistic and antagonistic responses, depending on the extent of foliar injury; antagonistic responses predominated when the injury was extensive. Similar results were obtained with pinto bean (Matsushima, 1971). Studies on grapes and apples (Shertz et al., 1980a, b) confirmed the observation that plants typically displayed an antagonistic response to the mixture when the injury from the individual gases was extensive. The relationship between the injury intensity from the individual pollutants and the type of response (antagonistic or synergistic) is shown in Figure 15.

The extent of foliar injury from the individual gases is important to consider when attempting to determine if the responses for the individual gases is greater than the summed effects of the individual ones. Synergism (greater than additive injury) occurred when the injury to soybean foliage from the individual pollutants was less than 45% (Heagle and Johnston, 1979); antagonism resulted when the injury from the single gases exceeded

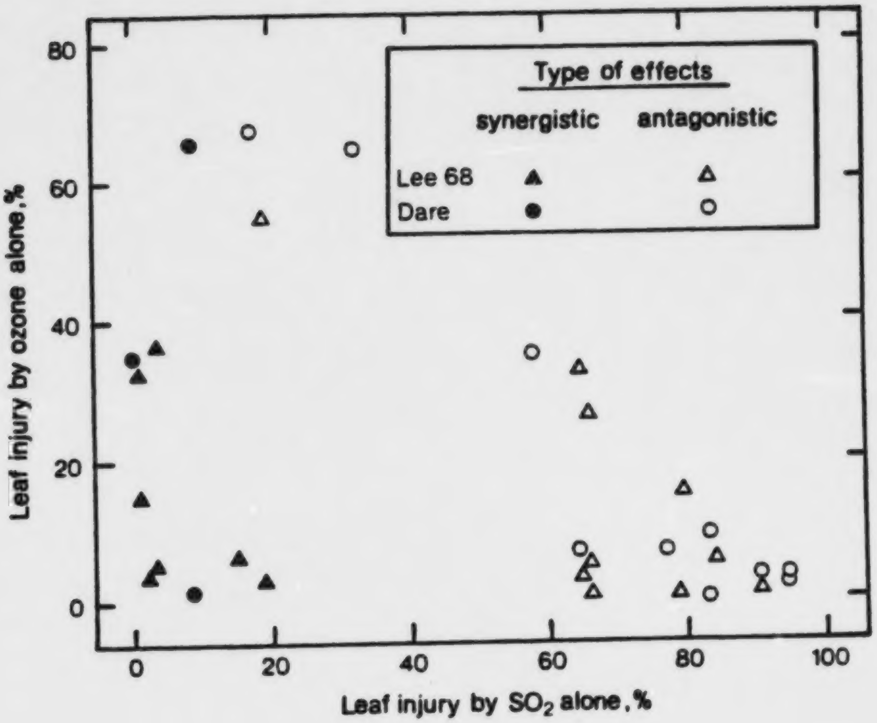

Figure 15. The relationship between the foliar injury intensity of two soybean cultivars as affected by various concentrations of O_3 and SO_2 and the nature of their interactive effects. Each symbol shows the coordinates for mean foliar injury, from O_3 and SO_2 singly, at which significant injury responses occurred in the corresponding mixture (Heagle and Johnston, 1979).

50 to 70%. In some cases the summed effects of the individual gases exceeded 100% which represents a mathematical not necessarily a biological antagonism. There have been only a few observations of antagonism when the injury amounts were small. The observations of antagonism are more common in growth than foliar injury responses.

5.2.4.2 Significance of External Growth Factors

As with O_3, various external growth factors can influence the severity of injury from exposures to combined pollutants. However, there have been too few reports concerning the influence of external growth factors to generalize about the responses. Through their influences on plant morphology and physiology, the external growth factors can influence pollutant uptake and its reaction within the plant directly, during and following exposure, and indirectly, prior to exposure.

Increasing light intensity during exposure to a mixture of O_3 and SO_2 increased the severity of injury to spinach (Yamazoe and Mayumi, 1977). Plants placed in the dark following exposure in the light were as severely injured as plants left in the light. Plants pretreated in the light or dark and subsequently exposed in the light were equally responsive to the pollutant combination.

Pinto beans exposed to a mixture of O_3 and SO_2 displayed the maximum injury at 15 C; the injury decreased with increasing temperature (Miller and Davis, 1981). The individual gases induced similar amounts of injury at both 15 and 32 C. The symptom expression changed with temperature. At 15 C the injury symptom was similar to SO_2, while at 32 C the injury was similar to O_3.

Ozone uptake and injury tend to increase with increasing relative humidity during exposure. A similar trend was observed in studies using mixtures of O_3 and SO_2. Carlson (1979) exposed young sugar maple, American ash, and black oak (Quercus velutina) plants to 0.05 ppm ozone and/or 0.5 ppm SO_2 at various relative humidities and light intensities and determined their effects on photosynthesis and visible injury. In general, the impact of the combined pollutants on photosynthesis and injury intensity was reduced at low relative humidities and low light intensities. However, the environmental conditions moderated the responses of the three tree species to the individual and combined pollutants differentially. Studies with three petunia cultivars (Elkiey and Ormrod, 1979c) showed that exposures to pollutant combinations at 50% RH caused a rapid increase in leaf resistance, suggesting stomatal closure, but at 90% RH there was only a slight increase.

5.2.4.3 Significance of Internal Growth Factors

The stage of leaf development and plant ontogeny have been shown to influence plant response to O_3 and PAN (compare Section 4.3). There have been only limited studies concerning the influence of leaf or plant development on the plant sensitivity to mixtures of O_3 and SO_2. At this time, there is no clear trend. In tobacco, the mature leaves (Menser and Heggestad, 1966) were most sensitive, while it is the middle-aged leaves of petunia cultivars that were most sensitive to injury from the pollutant combination (Elkiey and Ormrod, 1979c). The midshoot leaves of grape and apple were the most sensitive to the mixture (Shertz _et_ _al_., 1980a, b). Expanding and expanded peas leaves reacted differentially when exposed to lower concentrations of O_3 and SO_2 but at higher concentrations they responded similarly (Olszyk and Tibbitts, 1982).

5.2.4.3.1 Species, Cultivar, and Individual Plant Resistance

Extensive efforts have been made to determine the relative sensitivity ranking of plants to O_3 (see Chapter 4.3.2) and SO_2 (Van Haut and Stratmann, 1970). In comparison, there have been only a few studies on the responses of a range of species to mixtures of O_3 and SO_2. Individual studies have shown that species react differentially to combined pollutant exposures. However, there has not been a concerted attempt to develop listings of relative sensitivity to mixtures as there has been for the individual gases. Studies of herbaceous agricultural crops showed that broccoli and cabbage were least sensitive, while tobacco and radish were the most sensitive of the six species tested at three different concentrations of O_3 + SO_2 (Tingey et al., 1973d). Karnosky (1981) studied the relative sensitivity of 32 urban-tree cultivars, representing 11 species, to O_3 and SO_2 singly and in combination. Some cultivars of Acer platanoides, Acer rubrum, Acer saccharum, Fagus sylvatica, Fraxinus pennsylvanica, and Ginko biloba were tolerant to all three exposure combinations, while cultivars of Fraxinus americana and Platanus acerifolia were sensitive to all three exposures. However, all species and cultivars did not display the same sensitivity rankings to the individual and combined polluants. For example, Acer rubrum 'Bowhall' was highly sensitive to the combined polluants and displayed intermediate or resistant reactions to O_3 and SO_2, respectively. In contrast, Quercus robur was resistant to the combination and SO_2 but sensitive to O_3. The limited studies have not shown a clear similarity in the sensitivity to the combined and individual pollutants over a range of species and cultivars.

Not only do species respond differentially to mixtures of O_3 and SO_2 but cultivars and clones within species have shown differential tolerance. The response of several differentially susceptible (to ozone) tobacco species and cultivars to mixtures of SO_2/O_3 have been studied (Menser and Hodges, 1970; Grosso _et_ _al_., 1971; Hodges _et_ _al_., 1971; MacDowall and Cole, 1971; Menser _et_ _al_., 1973). Most types displayed different relative sensitivity rankings to ozone, the mixture of ozone plus sulfur dioxide and photochemical smog. In general, the effects of the combined gases was greater than for the individual pollutants.

Differential plant response in beans (33 cultivars) was studied using exposure to O_3 and SO_2 singly and in combination (Beckerson _et_ _al_., 1979). The O_3 injury among the cultivars ranged from 0 to 68% while, from the combination, injury ranged from 0 to 30%. Only two of the cultivars exhibited more than 10% injury from SO_2. The injury response between plants exposed to O_3 or SO_2 was not significant but the correlation coefficients for injury among the cultivars from the combination and either gas alone was highly significant, suggesting that the plant response to the mixture was the result of the reactions of both gases. In 29 of the cultivars, injury symptoms from the combined pollutants developed more slowly than the symptoms from O_3 alone. Not only was the rate of injury development different among cultivars but also the nature of the response was different. After 5 days of exposure, most of the cultivars showed more injury from O_3 alone than from the combination, but for the remaining cultivars injury was similar in both treatments.

The relative sensitivity ranking for three petunia cultivars was similar for O_3, SO_2, and their mixture (Elkiey and Ormrod, 1979b). However, for Elatior begonia cultivars, the plant response to O_3 and the combination were similar for some cultivars but different for others (Reinert and Nelson, 1980).

Six grass species, including 18 cultivars, exposed to mixtures of O_3, SO_2, and NO_2 (each at 0.15 ppm) displayed variable responses: the various cultivars of Kentucky bluegrass generally displayed a greater than additive response. The other five species displayed additive responses except for two cultivars which exhibited an antagonistic response (Elkiey and Ormrod, 1980b).

Karnosky (1976) studied the effects of O_3 and SO_2 singly and in combination on the foliar injury of five trembling aspen clones. The clones exhibited different patterns of sensitivity to the individual gases but exposure to the combined pollutants injured more ramets per clone and the percentage of leaves injured increased. There were variations in injury intensity among the clones.

The inheritance of differential tolerance to combined pollutants has been studied for two tree species. Repeatability studies with eastern white pine demonstrated that tolerance-sensitivity to the mixture of O_3 and SO_2 was under strong genetic control (Houston and Stairs, 1973). Plant responses to the effects of the combined pollutants correlated better with field observations than the responses from either pollutant individually (Houston, 1974). High success has been obtained in the field selection of trees displaying differential sensitivity to low or moderately high ambient levels of these pollutants. In trembling aspen, repeatability estimates, O_3 + SO_2 (0.464), O_3 (0.620), and SO_2 (0.642) illustrated that the responses to the individual and combined pollutants was under strong genetic control (Karnosky, 1977).

5.3 Ozone and Other Pollutants

There have been only a few reports concerning the effects of ozone in combination with other pollutants (either gases of heavy metals), making it difficult to draw general conclusions. However, for the gases the responses range from antagonistic to synergistic, while for the heavy metals the responses tend to be synergistic. Substantially more research will be needed to determine if these general conclusions are correct, especially for a range of plant species and environmental conditions.

5.3.1 Ozone and Nitrogen Dioxide

Matsushima (1971) showed that tomatoes and peppers exposed to either simultaneous or alternating mixtures of O_3 (0.4 ppm) and NO_2 (15 ppm) developed less injury than that caused by either gas alone. The addition of a nonphytotoxic level of NO_2 to O_3 increased foliar injury in rice, but decreased it in corn (Yamazoe and Mayumi, 1977). The addition of SO_2 to the $NO_2 + O_3$ mixture tended to decrease injury below that caused by the two-gas mixture. The sensitivity ranking of 12 clones of eastern white pine was the same following exposure to either ambient polluted air or to a combination of O_3 and NO_2 in the greenhouse (Nicholson and Skelly, 1977).

5.3.2 Ozone and Hydrogen Sulfide

The principal concern for this interaction was that H_2S is released from geothermal operations and synfuel plants which may be located near areas impacted with photochemical oxidants. Initial studies on the effects of H_2S on photosynthesis and leaf conductance showed that a low concentration of H_2S (0.74 ppm) stimulated both leaf conductance and photosynthesis but the addition of O_3 (0.072 ppm) significantly depressed both responses (Coyne and Bingham, 1978). Higher concentrations of H_2S inhibited both photosynthesis and leaf conductance while ozone intensified the effects. The effects of various concentrations of H_2S (0.30 to 7.0 ppm) in various combinations with O_3 (0.046 to 0.127 ppm) on leaf injury and plant growth and yield were studied (Bennett et al., 1980). The amount of foliar injury was similar in plots receiving H_2S or H_2S plus O_3. Predicted yield losses at a H_2S dose of 450 ppm·h showed that H_2S alone significantly reduced yield and the addition of O_3 caused a greater reduction in plant growth and yield.

5.3.3 Ozone and Heavy Metals

Zinc and cadmium reacted synergistically with ozone in producing visible injury and chlorophyll loss in garden cress (Lepidium sativum) and lettuce (Czuba and Ormrod, 1974). The combination of cadmium and O_3 induced the earlier development of necrosis and chlorosis and the injury was observed at lower O_3 and cadmium levels than for the individual treatments (Czuba and Ormrod, 1981). In tobacco and pinto bean, Cd (0.1 ppm) added to the soil interacted with O_3 (0.3 to 0.5 ppm) to produce an antagonistic response when visible injury, photosynthesis, and transpiration were measured (Faensen-Thiebes, 1981). Cadmium and nickel (concentrations 1, 10, 100 μmol) in the nutrient solution interacted to reduce root and shoot growth of peas (Ormrod, 1977). An ozone exposure increased the effects but the increase was less than additive. However, low concentrations of cadmium and nickel tended to enhance O_3 phytotoxicity. The interaction of cadmium and ozone was influenced by both concentration and the environmental conditions. Tomato plants grown at 0.25 and 0.75 mg Cd l^{-1} developed only slight foliar injury when exposed to ozone (0.20 ppm for 3 h) under cloudy skies and the Cd had no significant effect (Harkov _et al_., 1979). In full sun, there was extensive ozone injury and the joint response was synergistic. The changes in the cellular ultrastructure of pea leaves by exposure to ozone (0.50 ppm) were increased when plants were grown in nutrient solutions containing 100 μmol $NiSO_4$ (Mitchell _et al_., 1979).

The limited amount of published data indicates that heavy metals can increase the phytotoxic reactions of ozone. At present, it is not possible to assess the risk from the joint action of gaseous and heavy metal pollutants to vegetation, in industrial areas, along heavily traveled highways, or by the use of sludge as a fertilizer on crop lands.

5.4 PAN and Other Pollutants

As part of the photochemical oxidant complex, PAN co-occurs with ozone in the ambient air. In general, the plant response to combinations of PAN and O_3 at concentrations approximating ambient conditions were less than additive. Using a high PAN concentration (180 ppb), Kohut _et al_. (1976) showed that it interacted with O_3 synergistically when producing foliar injury on hybrid poplar. Sequential exposures produced more injury than exposures from the individual pollutants (Kress, 1972). Using a lower PAN concentration (50 ppb), the combination of PAN and O_3 induced less injury on ponderosa pine primary needles than did O_3 alone (Davis, 1977). In pinto beans, the response to the combined pollutants was additive or synergistic on the adaxial leaf surface, but antagonistic on the abaxial surface (Kohut and Davis, 1978). Simultaneous exposures to PAN and O_3 induced significantly less injury to petunia and kidney bean than either pollutant alone (Nouchi et al., 1983). In alternating exposures, O_3 alone induced as much injury as O_3 followed by PAN; PAN alone induced as much injury in petunia as a PAN exposure followed by O_3 (Nouchi et al., 1983). Combinations of PAN and O_3 generally produced less than additive effects on the growth of four tomato cultivars (Temple, 1982).

Studies concerning the effects of PAN and other pollutants that are not produced photochemically are very limited. In the laboratory, Matsushima (1971) exposed pinto bean, pepper (Capsicum frutescens) and tomato to mixtures of SO_2 (1.5 to 2.1 ppm) and PAN (0.27 to 0.40 ppm) and found that foliar injury ranged from additive to greater than additive. However, when the plants were exposed to alternating combinations of the individual gases, the injury was less than additive when compared to the injury caused by the same total exposure duration from the individual gases. The alternating exposure also caused significantly more injury than the simultaneous exposure.

5.5 Ozone, Sulfur Dioxide, and Acid Precipitation -- The Cause of Forest Decline in Central Europe?

Since the 1970's, in large areas of Central Europe there has been a dramatic decline in the health of forests, including disintegration of the stands. Initially, the term "Waldsterben," or forest decline, was primarily coined from emotional reactions shortly after a new type of forest injury was observed, however, the threat to the forests has now been clearly established. Based on a series of facts and circumstantial evidence, the primary cause of this injury appears to be ozone; in most locations it probably acts in combination with sulfur dioxide and acidic precipitation.

In so-called "clean air" locations, principally in southern Germany, injury symptoms have been observed mainly on white fir (Abies alga Mill.) during the last 10 years and since 1980 on Norway spruce (Picea abies L. Karst.). However, the symptoms were either different or only partially comparable to known epidemics and disease symptoms on forest trees (Rehbock, 1982; Schütt, 1982b; Rehfuess, 1983; Prinz et al., 1982; BML/LAI, 1982). A new type of injury syndrome, whose origin is not understood is found on the individual plant species.

5.5.1 Symptoms, Intensity, and Distribution of Injury

The type of injury on leaves, twigs, crowns, and roots varies among the tree species, locations and regions. Fundamentals of the principal syndrome will be described only for fir and spruce, the most threatened conifers, although other species, such Scots pine (Pinus silvestris), Douglas fir (Pseudotsuga menziessii), European beech (Fagus silvatica), and oaks also exhibit increased injury symptoms. For example, in individual cases with beech, the demarcation between the normal variation in the health of the stand is difficult to determine (Mülder, 1983).

5.5.1.1 Fir

Reports dating back several hundred years discuss the injury and death of firs, a species sensitive to various stresses, in Germany, Czechoslovakia, and Italy. According to Màlek (1981), the so-called fir death in central Europe was the consequence of explosive injury outbreaks that periodically occurred, almost simultaneously at several locations. In

Bohemia the interval between disease periods has become progressively shorter since the 1600s and within the last 50 to 100 years it has developed into a condition of permanent poor health and tree death. The injury is particularly intense following dry years, winters with low temperatures, or late frosts (Wagner, 1981). Since 1960 the injury intensity has increased. Current symptoms occur first and exhibit the most distinct impact on older trees (BML/LAI, 1982; SR-U, 1983). The needles, beginning with the older ones, show a light chlorosis, occasionally a dull discoloration, yellowing, and premature abscission. Typically, there is a progressive opening of the crown proceeding from bottom to top; the needles on the outer-most tips of the crown remain green the longest. The apical growth stops prematurely, consequently the firs display the characteristic "stork's nest" at an earlier stage of tree development. Parallel with the progressive needle loss, there is frequently an increased production of epicormic branches. With increasing injury, the "stork's nest" loses its contour and epicormic branches, indicating a disturbance in the water supply of the crown, and begins to die, reducing the tree's survival chances (Mülder, 1983). In injured but not yet dead crowns, the bark may become detached mainly near the base of the crown. At this stage, there are increased infections from bark beetles, Armillaria, and mistletoe. An additional characteristic is the pathological spread of watercore in the roots and lower trunk, where it may, finger-like, invade the sapwood (Schütt _et_ _al_., 1981a; Brill _et_ _al_., 1981; Lang, 1981; Blaschke, 1981a). A higher proportion of the fine roots die in diseased firs and spruces; also, the regenerative capacity of the fine root system is reduced, as is mycorrhizal formation (Hütterman, 1983; Blaschke, 1981a, b).

There is only partial correspondence between the symptoms of the current fir decline and "periodic re-occurring enigmatic disease of fir." The new symptoms of the current decline include (Wagner, 1981; Seitscheck, 1981, 1982; BML/LAI, 1982):

-- persistence for approximately 10 years with uncertain tendencies;
-- occurrence over the entire fir range but less intense in the Bavarian Alps;
-- rapid disease progress on individual trees;
-- frequently irreversible injury with a high proportion of tree mortality;
-- injury in different types of forest canopies and structures and at different types of sites.

In the firs' natural range, the earlier disease outbreaks occurred primarily on the eastern and northwestern edges of stands. However, in the current phase of the disease, trees in the natural range, growing in sites with optimum conditions, are affected (Seitschek, 1982). Severe disease outbreaks have occurred in the eastern and northeastern areas of the bavarian subalpine mountains, Bayrisher Wald, "Bavarian Forest"; Oberpfälzer Wald, "Upper Palatinate Forest"; Frankenwald, "Franconian Forest"; Fichtelgebirge as well as in the northern and middle Schwarzwald, "Black Forest," where more than 80% of the trees are diseased. When the disease progress rate is considered, and that 10- to 15-year-old firs are already affected (Schütt, 1982), then one must accept that a dramatic deterioration in the condition of the fir stands has occurred. The firs in Eastern Bavarian up to the Czechoslovakian border are threatened with complete loss. There have been reports of the fir decline in Poland (Sierpinski, 1981), Czechoslovakia (Màlek, 1981), Switzerland (Flühler and Bosshard, 1982), and Italy (Moreondo and Covassi, 1981), but the symptoms deviate to some extent among the various reports.

In the mountains, firs are ecologically and silviculturally valuable at the middle elevations. They root deeply in the forest subsoil and are well anchored against storms, thereby contributing significantly to stand stability, particularly when it includes shallow-rooted species such as the spruces. Concurrently, the firs extract nutrients from the deeper soil horizons, making nutrients available to the rest of the forest. The mixed alpine forest composed of fir, spruce, and beech are the most productive and valuable in Europe (Bonnemann and Röhrig, 1971).

5.5.1.2 Spruce

Only the most obvious injury symptoms, as observed in various regions, will be described. Increased needle fall spreading from top to bottom and erratically from the exterior to the interior causes a thinning of the crown over wide areas. Frequently there is a distinct dieback, particularly in the higher elevations of the Harz Mountains (BML/LAI, 1982). The injury usually occurs on the crowns of dominant trees which project above the general canopy level. The stand thereby loses the dominant members of its ecological support system; long-term structural destabilization is the probable consequence (Franz, 1983). In severely impacted mature trees that would normally display a substantial vertical growth the yellowing and casting of needles frequently begins beyond the first three or four needle whirls behind the tips (Mülder, 1983), thus the lower portion of the crown appears to have better needle retention. This symptom appears to be similar to the initial injury phase established for the decline and death of spruce experiencing chronic exposures from air pollution (Pelz and

Materna, 1964). The needle casting starts on the side branches at the transition between the upper and middle crown and spreads to the lower and upper portions of the crown (sub-top-dying).

A symptom more frequently found in southern Germany deviates from the above descriptions; the characteristic thinning of the crown proceeds from bottom to top and interior to exterior. The older trees, in general, display the so-called "Lametta syndrome"; the more or less denuded branches of the second order hang sleepily down, giving the trees a fringed or comb-like appearance.

The widely distributed yellowing of all needle ages is conspicuous, primarily on the upper sides of light-exposed branches; there is also a previously unobserved chlorosis on the tips of the older needles "Goldspitzigkeit" (Rehfuess, 1983; Zöttl and Mies, 1983; Bosch _et_ _al_., 1983). In addition to needle yellowing and loss, needle and branch anomalies were noted. Increased concentrations of abscisic acid and abscisic acid conjugates as well as changes in the composition of this metabolic group indicated a perturbation in phytohormone relations as observed in herbaceous plants subjected to various stresses (Schütt, 1983). Resin drops frequently occur inside and just below the crown area. Moreover, breaks occur in the stem bark within the crown and on the underside of the branches. Root deformation and loss is found in young spruce trees.

The spruce injury is most intense on the heights and ridge levels of the subalpine mountains, particularly in the Bayerischer Wald, "Bavarian Forest"; Oberpfälzen Wald, "Upper Palatinate Forest"; Fichtelgebirge; Frankenwald, "Franconian Forest"; Schwarzwald, "Black Forest"; Odenwald, Tannus; Spessart and Harz (BML/LAI, 1982). The injury is intensified at lower elevations (Zöttl and Mies, 1983). Increased injury has occurred on the spruce in Nordrhein-Westfalen, "North Rhein Westphalia," since the fall of 1982 (Prinz et al., 1982; Knabe, 1983). By and large, trees in the west and southwest are particularly impacted. Spruce in its natural habitat as well as in areas outside its natural range is injured. This wide occurrence of injury is alarming because until the latter half of the 1970s spruce was considered to be healthy and vigorous -- except in areas heavily impacted with SO_2. Spruce covers approximately 40% of the forested area in the Federal Republic of Germany and is economically the most important tree species. In the summer of 1982, it was estimated that about 10% of the area occupied by spruce stands was injured (BML/LAI, 1982). Since then, this percentage has clearly increased. At many locations, primarily in the higher elevations where fir are threatened with extinction, the spruce are not healthy either and there is no other comparable species with similar economic and ecologic characteristics available to replace it.

5.5.2 Investigations into the Cause of the Forest Injury

Given the current extent of forest injury and the progress rate of disease, it appears that extensive portions of the forests in Central Europe are endangered. As required for implementation of effective relief measures, intensive research into the probable causes has been initiated, e.g., natural conditions, silvicultural influences, and phytotoxic air pollutants.

5.5.2.1 Natural and Silvicultural Influences as Factors in the Cause of Forest Injury and Tree Death

Climate extremes and weather conditions are among the most likely natural causes that should be considered. In Central Europe, numerous observations have established that tree deaths may be caused by drought periods, cold years, a sudden drop in temperature during the winter, early or late frosts, or ice storms, acting at times either alone or in combination (Wagner, 1981; Seitschek, 1981). Severe injury occurs following extended droughts but only at particularly dry locations such as on shallow soils over a very permeable rock layer. Because forest injury occurs at well-watered sites and is widely distributed, drought periods must be excluded as the sole cause of injury (Schütt, 1977; BML/LAI, 1982). Drought can weaken trees, disrupt water relations (Schuck, 1981), and change their predisposition to biotic factors and air pollutants (Blaschke, 1981a, b; Schönborn and Weber, 1981). Drought may directly influence the spread of the pathological disorder "watercore" in diseased firs (Schütt, 1981a; Brill *et al*., 1981; Bauch, 1983).

Air pollution may also reduce the trees resistance to cold stress (Wentzel, 1965; Huttunen, 1980; Keller, 1981). However, several factors suggest that frost is not the primary injury cause; frost episodes did not occur at all injured sites and all frost-exposed locations did not exhibit increased injury (BML/LAI, 1982).

There have been extensive discussions to determine if and to what extent the growing of spruce as a monoculture beyond its natural range has contributed to the current problem. Also, to determine if previous forest use practices influenced the injury. The influence of stand structure can be excluded as the primary cause because both fir and spruce are injured independent of stocking rate and canopy structure. Injury occurs in both pure and mixed species stands and also in well managed and thinned forests. Conversely, there are, for example in the foothills and the edges of the Alps and on the upper Neckar, poorly thinned single-storeyed stands of old-growth firs that are presently healthy (BML/LAI, 1982; Mülder, 1983). Modifications in forest structure and management are not practical relief measures.

Spruces, particularly, have succeeded on sites outside their natural range. The injury to fir and spruce at different sites argues against unsuitable sites as the cause of the forest decline. There are natural stands of diseased spruce, for example at the higher elevations in the interior of the Bavarian forest, where the soils have exhibited an acidic reaction for an extended period and, in part, have a large humus accumulation. However, spruce on basic and, sometimes, on soils well bufferd with carbonate such as the "Parabraunerden" (a soil belong to the suborder Udolf), in the alpine foothills on gravel plains and on the calcareous soils on the alpine rivers (Mies and Zöttl, 1982) are also injured. Trees growing in areas receiving continual fertilization are injured while on highly reduced and consequently acid soils pure stands of healthy spruce are found. Liming the soils has not significantly reduced the needle loss (Aldinger, 1983). There is not a tight relationship between the injury intensity and the substrate characteristics or the stand nutrition (BML/LAI, 1982). Injury on fir is especially severe on sites with an adequate supply of nitrogen but pronounced Ca and Mg deficiencies (Evers, 1981; Rehfuess _et_ _al_., 1982; Zöttl and Mies, 1983).

There is broad agreement that monoculturing conifers, particularly spruce, on weakly buffered substrates with low cation exchange capacity increases the acidification of the upper soil layers, formation of a litter layer, and podzolization; consequently that the upper soil layers are depleted in soluble nutrients (Rehfuess, 1981b; Rehbock, 1982; Scheffer and Schachtschabel, 1982). Nevertheless, the widespread fear of a dramatic soil deterioration when conifers are monocultured has not been established (BML/LAI, 1982). Mülder (1983) has indicated that natural monocultures were as widely distributed as labile subclimax and stable climax forests.

Etiological studies have attempted to determine if animal pests or plant pathogens (viruses, mycoplasms, ricketsiae, bacteria, or fungi) are the cause or combined causes, of forest decline. Based on previous knowledge and the lack of typical distribution patterns that normally occur with pests and disease incidents, animal pests, pathogenic fungi, and bacteria were excluded as causes (Eichorn, 1981; Roll-Hansen and Roll-Hansen, 1981; Brill _et_ _al_., 1981). The locally increased infections from bark beetles and Armillaria, two typically weak parasites, resulted from a previous weakening of the host trees. Bacterial infections followed physiological disturbances and injury to the fine roots, including the mycorrhiza (Blaschke, 1981a), which, in fir, led to watercore formation in the roots and trunk (Schütt, 1981a; Brill _et_ _al_., 1981). The possible significance of root and stem nematodes as the primary cause of death in firs and spruces or animals as possible vectors for viruses, mycoplasms, or ricketsiae are unanswered (Schwenke, 1982). The prevailing opinion is that animal pests and phytopathogens are generally of secondary significance for the forest injury (Möhrig, 1983). However, there are contrary views (GVSt, 1982; Kandler, 1983; Frenzel, 1983).

5.5.2.2 Air Pollutants as the Cause of the Injury

Drought, frost, unfavorable edaphic conditions, poor site selection, failures in the structural composition of the forests and their uses are just as unsuccessful in explaining the sudden occurrence and dramatic deterioration in the health of the forest stands in Central Europe as infections from animal pests or pathogenic agents are. In individual cases, the various abiotic and biotic influences are certainly responsible for injury and as single or combined factors they contribute to the expression and the extent of injury. However, based on current knowledge they are excluded as the primary cause of the current phenomenon of "Waldsterben" or forest decline. Consequently, there must be an unknown allogenic factor that satisfies the following requirements:

-- distributed over several regions;

-- sudden occurrence, in high concentrations that are active over short durations, especially on the western sides of the mountain ranges;

-- a high biological activity.

With present knowledge, these conditions are only satisfied by specific air pollutants. However, a new category of pollution response must be present. The symptoms deviate from injury previously shown to be caused by acute or chronic exposures. By and large, there is a new syndrome occurring in the forests remote from emission sources, a circumstance that is similar to what previously occurred with photochemical oxidants in the United States (Berry and Ripperton, 1963; Miller *et al.*, 1963), that only later was linked to air pollution.

Given the degree of phytotoxicity, the concentration levels and spatial distribution, the ambient pollution complex of photochemical oxidants, SO_2, and acid precipitation should be considered as the most likely causes (Guderian and Rabe, 1982; Guderian, 1982; Arndt et al., 1982b; Prinz et al., 1982).

Previous concern was expressed regarding heavy metals, i.e., that they could present significant local risks for humans and animals as the metals moved through the food chain (Krause, 1974; Guderian et al., 1977; UBA, 1977; Prinz et al., 1979). The metals certainly demand increased consideration in light of the continuing need to protect the forests. In forest ecosystems the long-term input of heavy metals is a risk, particularly for the soil-dwelling organisms and for the release of nutrients from the litter. There is no evidence that heavy metal containing compounds alone or in combination are responsible for the forest decline (Zöttl and Mies, 1983). However, their mode of action raises fears (Keller, 1970) that they may, to some extent, cause acute injury over large areas. Accordingly, only photochemical oxidants and acid-containing sulfur compounds, the decisive portion of "acidic precipitation," remain as the potential cause of the injury.

While photochemical oxidants can directly effect only the aboveground portions of vegetation, acidic precipitation can also cause indirect effects through the soil, a concept proposed particularly by Ulrich (1981a, b, 1982). From the development of his "Ecosystem Theory" of forest decline, it follows that the natural coupling of biomass-production with acid use and biomass-decomposition with acid production in the forest is a consequence of acid deposition and the interference from man no longer in balance. The increased atmospheric input and acid production within weakly buffered soils ("pedogenic acidification") has led to the rapid decrease in the soil reaction to the buffer range of aluminum, a pH between 3 and 4;

consequently phytotoxic concentrations of metal ions are liberated. According to Ulrich, the forest decline is based on a series of processes, anthropogenic soil acidification, leaching of alkaline and alkaline-earth ions, disruption of litter decomposition, promotion of the podzolic processes, root injury from the toxic effects of Al and Mn ions, a reduction in the mass of fine roots, disturbance in the water relations of trees, leaf injury, crown drying, increased storm injury, and infections from pests and ultimately the death of trees. There is no disagreement about potential consequences of these effects but they are seen as long term. The "destabilization" of the forest ecosystem, postulated by Ulrich, can result from acidic precipitation alone when material import and export are no longer in equilibrium, in contrast to natural ecosystems not influenced by man. In the vicinity of individual pollution sources, following long-term exposure to elevated SO_2 concentrations, distinct reductions in soil pH have been established (Rusnow, 1919; Ewert, 1924; Guderian and Stratmann, 1962). However, for several reasons the forest decline phenomenon is not explained by direct effects through the soil.

The sudden appearance of injury and the rapid acute course of the disease implies a high injury potential. There is no proof in the literature that complex soil systems, at markedly different sites, in areas remote from industrial areas, can be so changed that within a few years the death of forests is the consequence. To be sure, there is probably a reduction in soil pH (Ulrich _et al_., 1979; Butzke, 1981; Evers, 1983; Reichmann and Streitz, 1983; Wittman and Fetzer, 1983), however, neither needle or bark analyses or studies of site conditions have provided evidence of Al or Mn toxicity on the diseased firs or spruces (Berchtold _et al_., 1981; Evers, 1981; Reiter _et al_., 1983; Bauch and Schröder, 1982;

Rehfuess, 1981a; Zöttl, 1983; Bosch _et al_., 1983). The occurrence of injury on firs and spruces growing on fluvents, a soil rich in carbonates (rendzina), for example on the steep limestone slopes of the upper Neckar, the Kalkalpen, and Schwäbischen Alp, "Swabian Mountains," as well as lithic pystrochrepts soils argues against Al and Mn toxicity (Rehfuess, 1981a; BML/LAI, 1982). To be sure, in most of the southern Schwarzwald, "Black Forest" the injured fir stands occur on acidic, rocky, brown soil types with a limited A_h-horizon (Mies and Zöttl, 1982). Following an analysis of the results from various countries, Zöttl (1983) concluded that Ulrich's postulated (1980, 1981a) Al toxicity to firs and spruces, in acidophilic conifer ecosystems, should be considered very unlikely. Also, disruption of litter decomposition causing a significant enhancement of podzolization cannot be unequivocally established (Abrahamsen, 1980; Rehfuess, 1981a). However, the long-term pollution-dependent input of materials must be considered as a serious danger to forest ecosystems. A series of inferences suggest that the atmospheric input of acids on weakly buffered sites has already influenced the availability of nutrient cation ions in the soil and their uptake through the plant (Zöttl and Mies, 1983; Bosch _et al_., 1983).

The concept that soil acidification and its consequences, resulting from either atmospheric input of acids or through the monoculture of conifers, is the sole cause of the previously described forest injury and decline cannot be supported. Consequently, one must acknowledge that the direct effects of air pollutants on the aboveground plant organs play a key role in the disease.

Since Stöckhardt (1871) established the phytotoxic characteristics of SO_2 more than 100 years ago, it has been considered to be the most important air pollutant, based on its extensive distribution. Decades of SO_2 exposure have induced injury, principally on conifer groves in industrial areas and their surrounding regions such as the Ruhr Valley (German Federal Republic), the area around Bitterfeld/Leipzig, the Erzgebirge, "Ore Mountains" (both in the German Democratic Republic and Czechoslovakia), the Böhmerwald, "Bohemian Forest" (Czechoslovakia), and in Oberschlesien, "Upper Silesia" (Poland). From this perspective, SO_2 has been considered as a possible cause of the forest injury. However, several observations argue against the concept that SO_2 is the main cause of forest decline, i.e., the occurrence of symptoms different than those typical of SO_2, several tree species from various taxa, and differential SO_2 resistance levels were impacted nearly simultaneously, the rapid progress of the disease including the death of individuals and complete stands and the ambient measurements of SO_2 concentrations. During the past few years, there have been some distinct increases in the peak SO_2 concentrations, especially in the so-called "clean air areas," particularly in eastern Bavaria near the borders with the German Democratic Republic and Czechoslovakia. Ambient measurements showed that the yearly mean SO_2 concentrations ranged from 10 to 36 $\mu g/m^3$ (0.0038 to 0.0137 ppm) but on a regional basis, the mean concentrations exhibited only a very slight increase (UBA, 1982; Landesanstalt für Umweltschutz, Baden-Würtemberg, 1981). The available dose-response relationships, established after decades of research, suggest that long-term mean SO_2 concentrations in this range pose only a slight risk to fir and spruce stands growing on extremely unfavorable sites (Guderian and Stratmann, 1968; VDI, 1978b; IUFRO, 1979, 1981; Wentzel, 1981). The fact that the lichen populations in areas of southern Germany exhibiting forest decline show little or no injury (Prinz et al., 1982) argues against the occurrence of sulfur dioxide in phytotoxic concentrations (see 2.6). When areas such as eastern Bavaria, which experience high acutely injurious SO_2 concentrations are ignored, it is apparent that SO_2 is not the sole cause of the new type of forest injury. The possible participation of SO_2, acting in concert with other pollutants, will be discussed.

Based on their distribution and phytotoxicity, photochemical oxidants should be considered as the initial cause of injury. The preliminary observations of Darley (1963/1964) established that ozone and PAN induced foliar injury on annual plants in Germany. In 1967, subsequent studies with tobacco plants established that phytotoxic concentrations of ozone occurred at several locations in the German Federal Republic (Knabe et al., 1973). Photochemical oxidant injury has been reported in other European countries (see 3.2.2). Guderian and Rabe (1983) in their report "Luftqualitätskriterien für Photooxidantien" (Air Quality Criteria for Photochemical Oxidants) for the Umweltbundesamt, Berlin, concluded that the established effects on plants and the existing measurements of ambient concentrations overlap, indicating that phytotoxic concentrations of photochemical oxidants that can endanger vegetation are widely distributed in the German Federal Republic. A comparison of the available ambient ozone measurements (see 1.3.2.2.1) and dose-response relations for vegetation (for example Table 24) supports this conclusion. The measured peak ozone concentrations [maximum half-hour mean values of up to 0.338 ppm (664 $\mu g/m^3$)] as well as mean values for longer time intervals indicate that ozone concentrations frequently exceed the tolerance level for vegetation Obviously the maximum peak concentrations generally occur in congested areas. However, when evaluating risks to vegetation, it should be remembered that anthropogenic ozone concentrations, in areas remote from pollution-emitting sources, may remain at elevated levels for longer periods because the low NO concentrations will only partially decompose the ozone. This ozone-frequency distribution yields high arithmetic mean concentrations (Prinz et al., 1982). Also the extended ozone-exposure time series reduces the duration of pollution-free periods that are important for plant recovery from pollution episodes (see 4.1).

As a probable cause of the new type of forest injury, ozone satisfies the three conditions mentioned earlier in this section: distribution over large regions, a high biological activity over a narrow range of concentrations, and ambient concentrations that fluctuate more with secondary pollutants than for primary ones. Repeatedly in the past few years, meteorological conditions in Europe have favored significant photochemical oxidant formation (1_____). In the time period 1966 to 1978, the emissions of nitrogen oxides, photochemical oxidant precursors, have increased in the Federal Republic of Germany from 2 to 3 million metric tons/year (UBA, 1981). In contrast, the SO_2 concentrations have remained approximately the same. Also by way of comparison, vertical profile measurements found high ozone concentrations several hundred meters above the ground corresponding with the particularly intense injury at these elevations (see 1._____). In this context, there are unanswered questions about the differential ozone resistance of individual European plant species (see 4.3.2).

Neither the direct effects of acidic precipitation on aboveground plant parts nor its indirect effects through the soil explain the new type of forest injury. Supporting this conclusion is decades of experience in areas exposed to high SO_2 concentrations and the fact that SO_2 emissions, which control the acidity of rain, have remained approximately constant at 3.5 million metric ton/year between 1966 to 1978 (UBA, 1981).

In principle, acidic precipitation can directly injure the cuticle or, following its penetration, be bioloically active within the leaf interior. The expression of effect is the consequence of the effective dose, that is to say the product of H^+-ion concentration and exposure duration as influenced by differences in plant morphology and wettability of the plant organs (Evans, 1980). The xerophytic conifer needles are significantly less susceptible to acidic precipitation (Haines et al., 1980) than the tender leaves of many angiosperms (Evans et al., 1977; Shriner, 1978). There have been no previous reports of cuticular injury on vegetation from areas in Central Europe exhibiting the forest decline. Scanning electron microscope studies on injured spruce needles found no significant cuticular injury but perhaps a premature loss of the wax plugs from the stomatal pore (Rehfuess, 1983). If cuticular injury occurs on conifer needles, it would be expected to develop first on the young, still developing needles as found by Wood and Bormann (1976). The small loss in epicuticular waxes on the needles of Scots pine (Fowler et al., 1980) in an area exposed to SO_2 are more likely the result of stress-induced changes in wax formation than the erosion of the cuticular waxes from the needle surface.

The nutrient supply (Ca, Mg, and, in some incidents, zinc) of the trees apparently plays a central role in the forest injury problem. Deficiencies of these elements, especially Mg, are widely distributed in injured forest stands (Zöttl et al., 1977; Altherr and Evers, 1977; Prinz et al., 1982). For example, in four-year-old needles from diseased spruce trees, Zöttl and Mies (1983) found an Mg content of < 0.20 ppt which was significantly less than the amount found in needles from visibly healthy trees. A similar relation was found by Zech and Popp (1983), the recent needles in the upper crown of diseased spruce trees contained 0.25 to 0.27 ppt Mg compared to 0.53 to 0.59 ppt in control samples from healthy trees. Visible Mg deficiencies develop on spruce when the Mg content of the needle tissue is less than approximately 0.35 ppt (Zech, 1968), leading Zech and Popp (1983) to conclude that an Mg deficiency was the principal cause of the chlorotic needle tip form of the disease causing the fir and spruce deaths on the acid granitic and phyllonitic soils of northeastern Bavaria. There have been three suggestions given for the cause of the deficiencies of Mg and other nutrients: a limited supply from the soil, restrictions in their uptake from the soil because of injury to the fine root system, and leaching of the minerals from the foliar organs.

The first evidence of an Mg-deficiency was found by soil and leaf analyses collected from a fertilizer study (established in 1958/1959) on beech growing on middle Buntsandstein (Lower Triassic) in the Odenwald (Altherr and Evers, 1974, 1977), a result that initially was not widely noticed. During the last few years it has been established that Mg and Ca deficiencies are widely distributed on acid soils leading to the conclusion that the atmospheric input of acidic compounds promoted the leaching of alkaline and alkaline-earth cations; also Mg deficiencies on vegetation are especially intense on Mg-poor substrates (Rehfuess, 1981a; Zech and Popp, 1983; Zöttl and Mies, 1983; Bosch et al., 1983). The increased mobilization of Mg from the sorption complex of acidic silicate soils has been found in the Solling area which has experienced heavy pollution exposures (Ulrich, 1981a) and also from experiments with artificial acidic rain (Abrahamsen, 1980). The extent to which the Mg-deficiency results from or is intensified by losses to the fine root network (Hüttermann, 1983) is unanswered. While Bauch and Schröder (1982) found an extremely low concentration of Ca and Mg in the xylem and cortical cells from the fine roots of diseased firs and spruces, Reiter _et al_. (1983) found no significant differences between healthy and diseased trees. Because the diseased trees generally have an adequate supply of nitrogen, phosphorus, and potassium, a general reduction in root biomass or root activity is not likely.

The leaching of nutrients from foliar organs has only recently been considered as the possible cause of forest injury, although there is extensive literature on leaching (Tukey, 1980). In addition to macro- and micronutrients, numerous organic substances such as sugars, amino acids, and phytohormones are leached. The nutrients, potassium, calcium, magnesium, and manganese, that occur in higher concentrations in the "apparent free space" can be leached in large amounts. Increased losses from the "inner space," i.e., symplastic transport, results from injury to the plasmalemma, tonoplast, and other biomembranes.

Artificial rain studies found that decreasing the pH increased the foliar leaching of potassium, calcium, and magnesium from sugar maple (Acer saccharum) and bean leaves prior to the appearance of tissue injury (Wood and Bormann, 1975). Also, studies with Norway spruce (Picea abies) and eastern white pine (Pinus strobus), using artificial rain, showed an increased leaching from the needles with a decreasing pH, however, the content of the corresponding nutrients remained unchanged in the needles (Wood and Bormann, 1976). In preliminary experiments, Prinz _et al_. (1982) found an increased leaching of Mg by artificial rain from spruce exposed to 0.50 ppm (300 $\mu g/m^3$) ozone for four weeks; the amount leached was pH-dependent. The observations of Evers (1981) supported the concept of nutrient leaching from needles. In June, shortly after the new growth reached full development, there were only slight differences in the calcium and magnesium contents among trees from different vigor (injury) classes, however, distinct differences were observed in the fall.

The extent to which foliar leaching in the injured forests is influenced by ozone (Arndt et al., 1982b) and acidic precipitation (Rehfuess, 1983) has not been determined. Certainly it will depend on the actual exposure intensity from the individual air pollutants. Given the available data concerning the mode of action of these compounds, it appears likely that acidic precipitation is primarily active in the "apparent free space," while ozone increases the permeability of biomembranes permitting the increased loss of nutrients and other substances from the cell interior. The combination of ozone and acidic precipiation therefore poses an important threat to the nutrient relations of plants.

As discussed above, the increased forest injury could result for ozone or the combined effects of ozone and SO_2. However, the injury intensity and the rate of disease progress, including the death of trees, are not explainable over large areas without considering a disruption in nutrient relations.

Analyses and evaluations of the available ambient air monitoring information, and biological and soils data suggest the following causes and consequences from the disease progress in the injured forests in Central European areas remote from pollution sources:

-- The available data support the hypothesis that the new type of forest injury occurring in areas of Central Europe, remote from pollution sources, is caused by photochemical oxidants, SO_2, and acid precipitation. The direct effect of ozone as a single agent and in combination with sulfur dioxide and acidic precipitation impairs the photosynthetic performance and water relations of forest trees with the consequence that vertical, radial, and especially root growth are reduced, as is the formation of mycorrhizae and the resistance of trees to biotic and abiotic stress factors.

-- Disturbances in nutrient relations, particularly Mg and Ca, enhanced the direct effect and increased susceptibility of trees to air pollutants and also climatic stresses and disease agents.

-- The deficiencies in these nutrients result, according to current knowledge, from an insufficient supply in the soil, a reduced uptake as a consequence of injury to the fine roots, and/or especially the leaching of the nutrients from the leaves as influenced by ozone and acidic precipitation.

-- There is little evidence for the hypothesis that acidic precipitation, in part in combination with soil acidification under coniferous monocultures growing outside their natural range, releases phytotoxic concentrations of Al. Also, there is no evidence that exposure to heavy metals causes the new type of forest injury.

-- Acidic precipitation and heavy metal-containing compounds pose a potential serious threat to soil productivity and therefore the health of the forests.

5.6 Summary

Plant response to pollutant mixtures can range from antagonistic to synergistic depending on the species, the specific pollutant mixtures, and concentrations, among other things. Our understanding of how environmental conditions modify these reactions is very limited. Based on available data, it is not possible to assess the influences of pollutant sequence, meteorological factors, cultural practices, or many other factors in relation to the joint action of pollutants on vegetation. The available data indicate that pollutant interactions do occur and they occur in the same concentration range as the compounds occur in the atmosphere. These observations are significant for environmental management, therefore better information concerning combined effects is needed. In pollutant-impacted areas, the ambient concentrations of the individual pollutants are generally low, so that at least an additive plant response to pollutant mixtures should be considered. This is especially true for subtle injury following chronic exposures to low concentrations. When establishing air quality criteria, one should consider not only the effects of individual pollutants, but also the possible effects of pollutant mixtures.

CHAPTER 6
DOSE-RESPONSE RELATIONSHIPS

In this chapter, experimental results concerning the quantitative relationship between the atmospheric concentrations of ozone and PAN and effects on higher plants will be described, documented, and evaluated. The goal is to establish the limits of vegetation impact from photochemical oxidants as a basis for risk prognosis and paving the way for remedial and mitigative actions. The principal concern is the most accurate identification possible of the lowest effective dose (i.e., concentration and exposure duration).

The derivation of such threshold values should be clear and verifiable because they have implications for the affected plant species and for the pollution source. Previous chapters concerning the nature and mechanism of injury, methods of detection and evaluation, as well as the decisive factors controlling plant responses provide a significant basis for the ascertaining the relationships between pollutant exposure and effect. Consequently, only a limited discussion of special methods is required, including the selection of experimental results as a basis for deriving air quality criteria and methods for summarizing individual values.

Only those experimental studies were considered that included the type and expression of injury on individual plant species or cultivars in relation to pollutant exposure, including concentration and exposure duration. Moreover, the measured responses must provide direct information concerning the impact on the useful value of the plants or permit the assessment of the indirect reduction in their useful values (see Section 3.3). The compilation of individual values for air quality criteria is based on the work of Jacobson (1977a), who reviewed numerous reports from controlled exposure studies to develop the concepts for determining limiting values and from the derivation of dose values for definite injury levels (Heck and Brandt, 1977; Linzon et al., 1975).

6.1 Dose-Effect Values from Gas Exposure Studies and Surveys in Pollutant Impacted Areas

The previous presentations of the relationships between pollutant exposure and effects have shown how strongly the genetic resistance level can vary in relation to plant development and external factors -- edaphic and climatic. Under these conditions, it is necessary for one to utilize data from several biological approaches, especially when it involves a complex pollutant mixture such as photochemical oxidants.

Results from the following types of pollutant studies were evaluated: fumigations in controlled environment chambers, greenhouse exposure chambers, field exposure chambers, with and without pollutant exclusion (air filtration) systems, and field studies. In reference to the presentations in Section 4.1 and 4.2, there is the general question of the applicability of the experimental results from such studies which deviate to varying degrees from natural conditions. Problems in the areas of cause and effect can also result from surveys of pollutant impacted areas and the observed effects cannot, unequivocally, be related to a specific cause or origin (Guderian, 1978). Conducting studies under various conditions can reduce these risks. The majority of the published data from experimental and epidemiological studies were evaluated within the context of the criteria concerning pollutant exposure and its effects on the useful value of the impacted plants. These evaluations were used for the derivation of the maximum acceptable ozone concentrations (see Table 24), the attainment of which should provide vegetation, in its various functions, reasonable protection from ozone effects. Because of space limitations, it was not possible to reiterate all studies which contained dose-response values. In the tabular material concerning ozone (Tables 16, 17, 20), only examples are presented. The examples were selected to illustrate the range and types of results that can be used to support the derivation of air quality criteria. A more detailed listing of dose-response values are contained in the publications prepared for the Umweltbundsamt, Berlin and the European Community, Brussels (Guderian and Rabe, 1982a, 1983) and the summary publications by Linzon et al. (1975) and EPA (1978a).

6.1.1 Dose-Effect Values from Pollutant Exposures

The importance of photochemical oxidants as phytotoxic air pollutants and their complex composition has resulted in extensive experimental investigations. The majority of these investigations were conducted with pot-grown plants in either the greenhouse or controlled-environment chambers. These methods with controlled pollutant exposure and varying degrees of climatic control have the advantage of greater reproducibility; they are particularly well suited for investigations of cause and effect and for hypothesis testing (compare 3.4).

The pollutant exposures were conducted in chambers with varying deviations from natural growth conditions. Using artificial light sources with a composition similar to daylight, representative plant reactions, at least for short term exposures at higher concentrations, can be established.

Foliar injury is a principal response criterion that is frequently, but not always, associated with growth reductions. Also, growth reductions may occur with no visible foliar injury symptoms (compare 2.5 and 3.3). In addition to foliar symptoms, there are other parameters which may be used to evaluate impacts, e.g., effects on the growth of leaves, shoots and roots, yield, pollen germination, pollen tube growth, photosynthate production, respiration, or rhizobium-induced nodulation in legumes.

For ozone, exposure durations ≤ 1 day (Table 16) and ≥ 1 day (Table 17), will differentiate between experimental results. Short term studies are concerned primarily with a single exposure on a single day; the longer-lasting exposures encompass exposure periods greater than a single day to several months or cover complete the vegetation period. The injurious concentrations vary over a wide range depending on individual plant species, cultivars, developmental stage, and external growth conditions. For ozone, the lowest limit for injury follows several hours of exposure to a concentration range of 0.02 to 0.05 ppm (Jacobson, 1977a).

In addition to the authors cited in Table 16, the dose-response values from the research of the following authors was considered. Adedipe et al. (1972a, 1973a), Adedipe and Ormrod (1974), Davis (1977), Davis and Kress (1974), Feder and Campbell (1968), Feder et al. (1969a), Houston (1974), Jacobson and Colavito (1976), Khatamian et al. (1973), Letchworth and Blum (1977), MacDowall and Cole (1971), Manning et al. (1972), Miller et al. (1974), O'Connor et al. (1975), Ormrod (1977), Ormrod et al. (1971), Pell and Brennan (1973), Proctor and Ormrod (1977), Shertz et al. (1980b), Tingey and Blum (1973), Tingey et al. (1973), Tingey and Reinert (1975), Townsend and Dochinger (1974).

In addition to the authors cited in Table 17, the dose-response data for exposure periods greater than 1 day from the following articles were evaluated: Barnes (1972a), Craker and Feder (1972), Dochinger and Seliskar (1970), Engle and Gabelman (1967), Feder and ampbell (1968), Heagle et al. (1974), Heagle et al. (1979c), Henderson and Reinert (1979), Hoffman et al.

Table 16. Effects of Defined Amounts of Ozone on Plants; Results from Short Term Exposures (≤ 1 d)

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect	Literature
28 Different Agricultural and Horticultural Species	0.25	1	acute foliar injury on 21 of 28 exposed plant species	Heck and Tingey, 1971
Radish (Raphanus sativus L.) Tobacco (Nicotaniana tabacum), Bel W3 and White Gold	0.075	2	acute leaf injury	
In addition to Radish and Tobacco also Tomato (Lycopersicon esculentum Mill.), Smooth Bromegrass (Bromus inermis L.), Oats (Avenua sativa L.), Lettuce (Lactuca sativa L.)	0.15	2	acute leaf injury	
White Clover (Trifolium repens L.) cv. Tillman	0.30	2	reduction in shoot dry weight, 17%; root dry weight 33% and nodule number 48%	Kochhar _et_ _al_., 1980
Tall Fescue (Festuca arundinacea Shreb.) cv. Kentucky 3)	0.30	2 (3x)	reduction in shoot dry weight, 22%; root dry weight, 27%	
9 Different Turfgrass Species and/or Cultivars (3 year old stand)	0.20	2	foliar injury on 5 of 9 grass species and cultivars	Richards _et_ _al_., 1980
Kentucky Bluegrass (Poa pratensis), 7 cultivars (3 year old stand)	0.10	3.5 h/day for 5 days	foliar injury on 6 of 7 cultivars	

(continued)

Table 16 (continued)

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect	Literature
19 Different Turfgrass Species and/or Cultivars	0.30	3	foliar injury on 14 of 19 grass species and cultivars	
Soybean (Glycine max. (L.) Merr.), 4 cultivars	0.15-0.30	1.5	threshold for foliar injury	Heagle, 1979a
	0.30-0.45	1.5	threshold for reduction of shoot growth	
Snap Bean (Phaseolus vulgaris L.)	0.30	2 x 1.5	up to 71% foliar injury to primary leaves and 36% on other leaves; plant dry weight reduced 10% and pod dry weight 12%	Blum and Heck, 1980
	0.60	2 x 15	up to 95% foliar injury to primary leaves and 68% on other leaves; plant dry weight reduced 25% and pod dry weight 41%	
Pinto Bean (Phaseolus vulgaris)	0.05	24	significant reduction in leaf growth	Evans, 1973
	0.10	12	significant reduction in leaf growth	
Tobacco (Nicotiana tabacum L.), Bel W3	0.10	5.5	in vivo and in vitro exposure reduced pollen germination 45% and pollen tube growth 50%	Feder, 1968

(continued)

Table 16 (continued)

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect			Literature
				Ives	Delaware	
Grapevine (Vitis labrusca, Bailey), 2 cultivars	0.40	4	leaf injury	27%	1%	Shertz et al., 1980a
			reduced shoot growth	40%	17%	
			premature leaf drop	5%	--	
	0.08	4	leaf injury	67%	56%	
			reduced shoot growth	60%	33%	
			premature leaf drop	15%	--	
18 Different Coniferous Tree Species	0.10	8	needle injury on Austrian pine (Pinus nigra Arnold), jack pine (Pinus banksiana Lamb.), and Virginia pine (Pinus virginiana Mill.)			Davis and Wood, 1972
	0.25	4	needle injury on Austrian pine (Pinus nigra Arnold), jack pine (Pinus banksiana Lamb.), and European larch (Larix decidua Mill.)			
	0.25	8	needle injury on all 8 coniferous species			

Table 17. Effects of defined amounts of ozone on plants; results from chronic exposures (≥ 1 d).

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect	Literature
Winter Wheat (Triticum aestivum L.)	0.10	54 days 7 h daily	seed yield reduced: container grown 10% field grown 16%	Heagle *et* *al*., 1979e
	0.13		seed yield reduced: container grown 27% field grown 33%	
Corn (Zea mays L.)	0.03	60 days, 5.5 h daily	no effect on pollen germination	Mumford *et* *al*., 1972
	0.06	60 days, 5.5 h daily	pollen germination reduced about 50%	
	0.12	60 days, 5.5 h daily	pollen germination reduced about 60%	
Corn (Zea mays L.) Golden	0.05	64 days, 6 h daily	14% leaf injury, seed weight reduced about 9%	Heagle *et* *al*., 1972
	0.10	64 days 6 h daly	25% leaf injury, seed dry weight reduced about 45%	
Orchardgrass (Dactylis glomerata), perennial ryegrass Lolium perenne)	0.09	5 weeks, 5 days/week, 4 h daily	some leaf chlorosis, shoot dry weight reduced 14 to 21%	Horsman *et* *al*., 1980
Tall fescue (Festuca sp.)	0.08	6 weeks	leaf dry weight reduced about 17%, shoot dry weight reduced about 15%, and tillering about 8%	Johnston *et* *al*., 1980

(continued)

Table 17 (continued)

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect	Literature
Crimson Clover (Trifolium incarnatum) and	0.03 8 h daily	6 weeks,	yield reduced < 10%, not significant	Bennett and Runeckles, 1977
Italian ryegrass (Lolium multiflorum) as monocultures and as a mixture	0.09	6 weeks, 8 h daily	reductions in monocultures Crimson Clover: leaf area, 50%; yield (dry weight), 36% Italian Ryegrass: leaf area, 35%; yield (dry weight), 36% reductions in the mixture of Crimson Clover and Italian ryegrass: leaf area, 26%, yield (dry weight), 22%	
Alfalfa (Medicago sativa L.)	0.05	68 days, 7 h daily	shoot dry weight reduced 30 and 50% for the 1st and 2nd harvests, respectively	Neely et al., 1977
Potato (Solanum tuberosum L.) 2 cultivars	0.20	6 x 3 h biweekly	Norland 1977 1978 reduction in tuber number 19% 21% reduction in tuber weight 30% 20% Kennebeck reduction in tuber number 40% 32% reduction in tuber weight 54% 30%	Pell et al., 1980

(continued)

Table 17 (continued)

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect	Literature
Soybean [Glycine max. (L.) Merr.], Corsoy	0.064	55 days, 9 h daily	seed yield reduced about 31%	Kress and Miller, 1981
	0.079		seed yield reduced about 45%	
	0.094		seed yield reduced about 56%	
Soybean (Glycine max. (L.), Merr.), 4 cultivars	0.06-0.09	10 days, 6 h daily	visible injury on all 4 cultivars, primarily chlorosis	Heagle, 1979a
	0.09-0.12	10 days, 6 h daily	shoot growth of 2 cultivars reduced	
Pinto Bean	0.06	40 days, 5 days/week	height growth reduced about 26%, shoot and root dry weights 48 and 50%, respectively, rhizobium nodule number and weight reduced about 45 and 74%, respectively	Manning, 1978
Radish (Raphanus sativus L.)	0.05	5 weeks, 5 days/week, 8 h daily	plant dry weight reduced about 31%, root fresh weight and leaf fresh weight about 54 and 20%, respectively	Tingey *et al.*, 1971
Spinach (Spinacia oleracea L.), 11 cultivars, values are the mean of 11 cultivars	0.06	37 days, 7 h each	leaf necrosis 6%, reductions in fresh weight container grown 4% field grown 18%	Heagle *et al.*, 1979b

(continued)

Table 17 (continued)

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect	Literature
	0.10	37 days, 7 h each	leaf necrosis 38%, reductions in fresh weight container grown 25% field grown 37%	
	0.13	37 days, 7 h each	leaf necrosis 65%, reductions in fresh weight, container grown 65% field grown 69%	
Cotton (*Gossypium hirsutum* L.), Alcala SJ2	0.25	15 weeks, 2 x weekly for 6 h each	reduced weight for open bolls about 60%, seeds about 60%, and ginned fibers about 62%	Oshima *et al*., 1979
	0.25	22 weeks, 2 x weekly for 6 h each	reduced weight for open bolls about 59%, seeds about 60%, and ginned fibers about 59%	
Petunia (*Petunia hybrida* L.)	0.05-0.07	53 days, 24 h daily	flower fresh weight reduced about 30%	Craker, 1972
Carnation (*Dianthus caryophyllus* L.)	0.05-0.09	90 day, 24 h daily	leaf tip necrosis; reduced vegetative growth, and flowering reduced about 50%	Feder, 1970a
Geranium (*Pelargonium hortorum* Bailey)	0.07-0.10	90 days, 9.5 h/day	leaf chlorosis and leaf drop; reduced vegetative growth, flowering reduced 50%, and decreased flower retention	

(continued)

Table 17 (continued)

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect	Literature
Ponderosa Pine (Pinus ponderosa)	0.15	10 days, 9 h daily	reduction in apparent photosynthesis about 4%	Miller et al., 1969
	0.15	20 days 9 h daily	reduction in apparent photosynthesis about 25%	
	0.15	60 days 9 h daily	reduction in apparent photosynthesis about 34%	
	0.30	10 days 9 h daily	reduction in apparent photosynthesis about 12%	
	0.30	20 days 9 h daily	reduction in apparent photosynthesis about 50%	
	0.30	30 days 9 h daily	reduction in apparent photosynthesis about 72%	
	0.45	30 days 9 h daily	reduction in apparent photosynthesis about 85%	
Sugar Maple (Acer saccharum Marsh)	0.05	2 days, 7-11 h daily	net photosynthesis reduced about 30%, 21%, and 0%, for the three cultivars, respectively	Carlson, 1979
Black Oak (Quercus velutina Lamb.)	0.05	1 week, 7-11 h daily	net photosynthesis reduced about 48%, 27%, and 0%, for the three species, respectively	

(continued)

Table 17 (continued)

Plant Species	Concentration ppm	Exposure Duration h	Type and Intensity of Effect	Literature
White Ash (Fraxinus americana L.)	0.05[1]	3 weeks, 7-11 h daily	net photosynthesis reduced about 34%, 55%, and 6%, for the three species, respectively	
Conifer Species	0.10	20 weeks, 6 h daily	the most severe foliar injury occurred on ponderosa pine (20%), lodgepole pine (16%), and shore pine (13%), significant growth reduction occurred in ponderosa pine and eastern white pine	Wilhour and Neely, 1977
Yellow Poplar (Liriodendron tulipifera L.)	0.10	6 weeks, 12 h daily	reduction in relative growth rate about 37%, relative leaf area growth rate about 34%, and net photosynthesis about 17%	Jensen, 1981b
Eastern Cottonwood (Populus deltoides Bartr.)			reduction in relative growth rate about 59%, relative leaf area growth rate about 52%, and net photosynthesis about 58%	

(1973), Hoffman et al. (1973), Jensen (1973), Mass et al. (1973), Manning and Vardaro (1974a, 197b), Ogata and Maas (1973), Oshima (1973), Oshima et al. (1975), Price and Treshow (1972), Reinert and Nelson (1979), Shannon and Mulchi (1974), Tingey et al. (1973c), Tingey and Reinert (1975), Wammsley et al. (1980).

The limited number of experimental PAN exposures are presented in a single table (18), including exposure periods longer than 24 hr. The lowest PAN concentration that caused foliar injury on petunia was 7 ppb for 8 hr (Nouchi, 1979).

6.1.2 Dose-Effect Values from Field Studies and Pollutant Impacted Areas

Surveys of dose-effect relationships in field studies or pollutant impacted areas have significant advantages. In contrast to the extrapolation problems from controlled pollutant exposures, the experimental results are representative of the location and may be generalized to areas with similar soil and climatic conditions. Also, the frequent use of response data relating to reductions in useful values of plants as response criteria in these studies is advantageous. Nevertheless, there are difficulties, namely the identification and evaluation of the injurious components and confounding factors, the determination of the pollutant dose and the establishment of the damage intensity (Table 20).

To determine pollutant exposure, ozone is usually measured; total oxidants are measured less often. A lack of reliable monitoring techniques that can relate total oxidants concentrations to vegetation effects contributes to these limited measurements. The exposure dose can be determined more or less exactly from information on the ozone frequency distribution at specific concentration ranges (e.g., Table 19). Lefohn and

Table 18. Effects of Defined Amounts of PAN on Plants; Results from Controlled Exposures

Plant Species	Concentration ppb	Exposure Duration h	Type and Intensity of Effect	Literature
Petunia (Petunia hybrida Vilm.)	100	5	severe foliar injury	Stephens *et* *al*., 1961
Pinto Bean (Phaseolus vulgaris L.)	100	5	moderate foliar injury	
Petunia, Tomato	14	4	foliar injury (field observations)	Taylor, 1969
Petunia (Petunia hybrida Vilm.)	140	1	33% foliar injury	Taylor, 1969
Pinto Bean (Phaseolus vulgaris)	140	1	55% foliar injury	
	40	4	90% foliar injury	
	20	8	44% foliar injury	
Petunia, Tomato, Dwarf Meadowgrass, Romaine Lettuce	15-20	4	"may be severely damaged ... in the polluted atmosphere"	Taylor and McLean, 1970
Petunia (Petunia hybrida)	200	1/2	74 injury index, scale 0 - 500	Drummond, 1972
	100	1	97	
	50	2	116	
Petunia (Petunia hybrida Vilm.), 6 Cultivars	120	1	a trace to slight foliar injury on 5 of 6 cultivars	Feder *et* *al*., 1969a
	250	1	a trace to moderate foliar injury on all 6 cultivars	

(continued)

Table 18 (continued)

Plant Species	Concentration ppb	Exposure Duration h	Type and Intensity of Effect	Literature
	500	1	slight to moderate foliar injury on all 6 cultivars	
Petunia (Petunia hybrida Vilm.) cv. White Casdade	150	1.5	24% foliar injury	Pell and Gardner, 1979
Petunia	32 14 7	1 3 8	leaf injury threshold concentration for each combination of concentration and duration	Nouchi, 1979
Pinto Bean (Phaseolus vulgaris L.)	150	3	21% foliar injury	Pell, 1976
Bean (Phaseolus vulgaris L.), cv. Provender	80	0.5	disruption in plant water relations	Starkey et al., 1981
Pinto Bean (Phaseolus vulgaris L.)	50	4	mild foliar injury, primarily abaxial bronzing with light bifacial necrosis	Kohut and Davis, 1978
Chard, Spinach, Japanese Radish, Kidney Bean, Tomato, Lettuce	100	6-10	foliar injury	Nouchi et al., 1975
Petunia	30	6-10	foliar injury	
Lettuce (Lactuca sativa L.) cv. Empire	20	2 x weekly, 4 h each from seedling to maturity	reduction in leaf fresh weight	Taylor et al., 1981 (cit. in Temple, 1982)

(continued)

Table 18 (continued)

Plant Species	Concentration ppb	Exposure Duration h	Type and Intensity of Effect	Literature
	40	2 x weekly, 4 h each from seedling to maturity	reduction in leaf fresh weight	
Lettuce (Lactuca sativa L.) cv. Empire	50	1 x weekly, 4 h, 3 to 4 weeks	15% foliar injury, no effect on growth	Temple, 1982
Tomato (Lycopersicon esculentum L.)	50	1 x weekly, 4 h, 3 weeks	significant reductions in plant height, leaf and root dry weights, but no foliar injury	
Maple, Ash, Locust, and Oak spp.	200-300	8	differentially severe injury depending on the age-dependent susceptibility	Drummond, 1971
Little Leaf Nettle (Urtica urens L.)	50	5 x 7 h	20% foliar injury	Posthumus, 1977
	50	9 x 2 h	12% foliar injury	
Annual Bluegrass (Poa annua L.)	50	6 x 7 h	3% foliar injury	
	50	9 x 2 h	2% foliar injury	

Table 19. An example of selected ozone frequency distributions from several sites in California (EPA, 1979).

County	Hourly ozone concentrations µg m^{-3} Percentile 10	30	50	70	90	95	99	Max	Integrated[1] Exp. Index (µg m^{-3} h)
Riverside	10	10	20	39	176	255	372	725	208808
Kern	10	20	39	59	137	176	216	294	50070
Fresno	10	10	20	59	118	137	196	294	20031
Merced	10	20	39	59	118	137	196	274	19447
Sacramento	10	20	20	59	98	137	216	431	35082

[1] Calculated according to the method of Lefohn and Benedict (1982).

Benedict (1982) developed an "integrated Exposure Index" that expressed the frequency distribution as a single value that the authors believed could be related to plant response.

The precision with which effects are established depends on the type of field study. Investigations in open-top (for example, MacLean and Schneider, 1976; Heggestad et al., 1980) or closed-top (for example, Thompson and Taylor, 1969) chamber systems with regulated pollutant addition systems or filtered and unfiltered ambient air exposures allow a precise determination of effects, i.e., growth or yield. However, with surveys of cultivated or native plants (for example, Brennan and Rhoads, 1976; Mosley et al., 1978) without similar chambers, one should not expect comparable results because a "control" is lacking.

The data in Tables 20 and 21 were developed using various experimental designs and ozone monitoring techniques. Different measures of growth and yield have been used; it is not clear if these different response measures are equally susceptible to ozone. The ozone exposure methods included: ambient air, ambient air with supplemental ozone additions, and ozone additions to charcoal filtered air. However, most ozone exposures resulted from the constant ozone addition for fixed time periods, producing highly artificial exposure regimes. A wide range of ozone concentrations and exposure durations were used. Although the published reports usually contain the concentration, duration, and sometimes exposure frequency, the number of exposures, the diurnal timing of exposures, and the plant development stages are not given. In some studies the plant received "square wave" (cconstant ozone concentrations for a fixed time period) exposures interspersed with pollutant-free periods of a few hours to several days, while in other studies variable concentrations were used

Table 20. Effects of Defined Amounts of Oxidants (Ozone) on Plants; Results from Studies in Polluted Areas

Plant Species	Concentration ppm	Exposure Duration	Type and Intensity of Effect	Literature
Corn (Zea mays L.), 2 cultivars		68 days from germination to harvest	on "Monarch Advance," the ozone-sensitive cultivar the yield (dry weight) was reduced about 58%; also there was no foliar injury, premature chlorosis and senescence; on "Bonanza," the ozone-resistant cultivar, the yield (dry weight) was reduced about 44% with slight foliar injury	Thompson *et al.*, 1976a
	< 0.08	467 = 43.4%		
	0.08-0.16	366 h = 33.3%		
	< 0.06	266 h = 24.3% of light period from 600 21.00 h		
Potato (Solanum tuberosum)	≥ 0.05	326-444 h in 2 years	yields reduced about 34-50% (2 years for 2 cultivars)	Heggestad, 1973
			20-26% (1 year for 2 cultivars)	
Alfalfa (Medicago sativa L.), 2 cultivars		monthly mean, proportion of light period	mean reduction in forage 33 to 42% and reductions in crude fiber, β-carotene, and vitamin C in both cultivars	Thompson *et al.*, 1976b
	> 0.08	∼ 50%		
	> 0.12	∼ 30%		
	> 0.16	∼ 20%		

.(continued)

Table 20 (continued)

Plant Species	Concentration ppm	Exposure Duration	Type and Intensity of Effect	Literature
Bush Bean, 4 cultivars	≥ 0.10	from seedling to harvest, 60 days, 1 to 40 h	yield reductions between open-top chambers with without air filtration ranged between 5 and 27% and premature leaf drop on oxidant sensitive cultivars during the growth periods of 1972 to 1976	Heggestad et al., 1980
	≥ 0.05	~ 250-480 h, in Beltsville, Maryland, during the growth periods 1972-1976, 2 plantings each year		
Bush Bean (Plaseolus vulgaris L.), cv. Tendergreen	0.041 (daily mean (0.017-0.09 (variation about daily mean)[1]	43 days	reduction in the number and weight of marketable beans, about 24 to 26% compared to the controls which received 60-70% less oxidant exposure	McLean and Schneider, 1976
Tobacco (Nicotiana tabacum), Bel W3	0.02-0.03	6-8 h	trace of foliar injury	Heck and Dunning, 1967
Orange (Citrus sinensis Osbeck)	> 0.10	148 h monthly average, from March to October; 254 h monthly average from July to September	yield reduced 54%	Thompson and Taylor, 1969
Navel Orange	0.00-0.69[2] 0.02-0.67[3]	8 months from blossom to harvest	increased leaf and fruit drop; significant reduction in fruit yield in the absence of visual injury[4]	Thompson et al., 1972

(continued)

Table 20 (continued)

Plant Species	Concentration ppm	Exposure Duration	Type and Intensity of Effect	Literature
Eastern White Pine (Pinus strobus)	> 0.03	10-15 h continuously	chlorotic fleck on new needles	Linzon, 1973
Ponderosa pine (Pinus ponderosa)	> 0.15	2 h daily over 2 months	"chlorotic decline	Miller et al., 1969

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[1] Oxidant concentration.

[2] Measured peak oxidant concentrations.

[3] Measured maximum hourly average of oxidant for individual months.

[4] In experiments units with filtered ambient air and comparable O_3 concentrations, there was less damage observed; additional evidence that other compounds of photochemical smog, i.e., PAN and NO_x, increase the ozone toxicity.

during the ozone exposure periods. In most of these studies, the ozone exposures were characterized by a mean concentration, however, other exposure parameters have been used (Jacobson, 1982). The use of a mean concentration is not reliable because it assumes that all products of time and concentration produce equal effects, an assumption which has not been verified by research (see Chapter 4.1). Also, there is no direct, verified method to relate mean ozone concentrations or the results of most experimental exposures to ambient pollutant regimes. Jacobson (1982) summarized the experimental approaches to determine ozone effects on crop productivity and concludes that the studies are rarely performed or described in terms that can be compared to ambient air quality standards. Despite these confounding factors and limitations, the data in Tables 20 and 21 are the best available to describe ozone effects on plant growth and to establish limiting values to protect plants from growth and yield losses.

The data in Table 20 are only examples as in Tables 16 and 17. Also, the work of the following authors was considered: Bell and Cox (1975), Bisessar and Temple (1977), Brasher _et_ _al_. (1973), Brennan and Rhoads (1976), Cameron _et_ _al_. (1970), Heagle _et_ _al_. (1973), Howell _et_ _al_. (1976), Mosley _et_ _al_. (1978), Thompson and Kats (1970), Thompson _et_ _al_. (1969), Thompson and Taylor (1969), Weaver and Jackson (1968).

6.2 Methods to Derive Limiting Factors

The level of certainty for limiting values depends on the amount and quality of data and the models used to evaluate it (Jacobson, 1977a). The method for deriving limiting values is based on these criteria. The models should describe, with reasonable accuracy, the relationship between exposure and effect. Limiting values are generally useful for establishing

Table 21. Percent yield reduction as a function of ozone concentration[a] (Heck *et al.*, 1982).

Crop	Linear Function[b]	Predicted % Yield Reduction at Two O_3 Concentrations[d] (± SE) 0.06 ppm	0.10 ppm
Corn (Coker 16)	Y = -2.7 + 108x	3.83 ± 1.0	8.1 ± 2.1
Soybean (Corsoy)	Y = -15.5 ± 621x	21.7 ± 1.4	46.5 ± 2.9
Soybean -- 1977 (Davis)	Y = -11.1 + 443x	15.5 ± 2.4	33.2 ± 5.1
Soybean -- 1978 (Davis)	Y = -8.8 ± 353x	12.3 ± 3.6	26.4 ± 7.7
Kidney Bean (Calif. Light Red)	Y = -4.8 ± 193x	6.8 ± 1.3	14.5 ± 2.8
Lettuce, Head (Empire)	Y = -16.3 ± 652x	22.8 ± 1.7	48.9 ± 3.6
Peanut (NC-6)	Y = -17.8 ± 711x[c]	24.9 ± 0.7	53.3 ± 1.5
Spinach (America)	Y = -13.2 + 527x	18.5 ± 3.0	39.6 ± 6.4
Spinach (Hybrid 7)	Y = -13.0 ± 517x	18.1 ± 3.7	38.9 ± 8.0
Spinach (Viroflay)	Y = -14.8 + 594x	20.7 ± 3.1	44.4 ± 6.6
Spinach (Winter Bloomsdale)	Y = -14.9 + 599x	20.9 ± 3.4	44.8 ± 7.3
Turnip (Just Right)	Y = -22.1 ± 887x[c]	31.0 ± 2.1	66.4 ± 4.5
Turnip (Purple Top White Globe)	Y = -20.5 + 817x[c]	28.6 ± 2.4	61.4 ± 5.0
Turnip (Shogoin)	Y = -20.5 ± 818x	28.6 ± 2.6	61.4 ± 5.5
Turhip (Tokyo Cross)	Y = -19.1 + 763x[c]	26.8 ± 4.6	57.4 ± 9.8
Wheat (Blueboy II)	Y = -7.4 + 290x	10.4 ± 1.4	22.3 ± 3.0
Wheat (Coker 47-27)	Y = -10.1 + 405x	14.2 ± 1.2	30.4 ± 2.6
Wheat (Holly)	Y = -7.5 + 304x[c]	10.6 ± 1.5	22.6 ± 3.3
Wheat (Oasis)	Y = -6.2 + 250x	8.7 ± 1.7	18.6 ± 3.7

[a] This includes all data sets. The O_3 is expressed as the seasonal 7-h/day mean concentration.

[b] $Y = \frac{100b_1}{a}[0.025 - x]$

where Y = predicted percent yield reduction, b_1 = the regression coefficient from the yield model, a = the predicted yield at a seasonal 7-h/day mean O_3 concentration of 0.025 ppm, and x = seasonal 7-h/day mean O_3 concentration.

[c] These models must be considered with caution. More complex models account for significantly more of the variation than these simple linear models. Compare the predicted percent yield reductions for the plateau-linear model at 0.06 ppm to get an idea of the differences.

[d] Values may differ slightly from those predicted by the equations due to a rounding of numbers in the functions shown. The 0.06 ppm seasonal 7-hr/day mean O_3 concentration is the maximum mean concentration expected in many parts of the U.S. when the one-hr standard of 0.12 ppm is just met; the 0.10 ppm was arbitrarily used as a maximum 7-hr/day mean O_3 concentration for comparison.

air quality criteria and they also allow the evaluation of the phytotoxic risk potential from measured exposure concentrations and may assist in remedial or mitigative actions.

With present knowledge, the following two models are suited for the stated role: (1) the concept of determining limiting values; and (2) the determination of specific doses that cause specific injury levels. Both models are suited for short term effects from acute injurious concentrations. However, for intermittent and long duration exposures at low concentrations, both methods are deficient. At present, the data are lacking to develop and use such models.

6.2.1 Determination of Limiting Values

The concept of limiting values elaborated by Jacobson (1977a) during his presentation to the VDI-Congress, "Ozon und seine Begleitsubstanzen im photochemischen Smog" at Düsseldorf (1976) resembles the models of McCune (1969) for fluorides and Larsen and Heck (1976) for ozone and sulfur dioxide, singly. The objective of these models is to determine the boundary conditions between doses that are probably injurious and those that are not.

Limiting values for ozone and PAN (Figures 16-18) were developed from studies conducted in the USA that contained definite information concerning pollutant concentration and duration of exposure. Each study was represented by a point in the coordinate system representing the lowest concentration and duration of exposure used in the study that induced foliar injury symptoms. The data sets used did not necessarily establish an injury threshold which would prevent foliar injury if obtained, because the data sets reflected the limitations in measurement and experimental techniques. In addition, it is possible to establish only the injuriousness of an exposure but not the harmlessness. Despite extensive investigations, it is still possible that combinations of conditions that were previously thought to be harmless can now be shown to cause injury. It follows that the derivation and the subsequent observance of limiting values will produce a high but not an absolute guarantee of protecting vegetation; a small risk will remain.

As a response criterion, Jacobson (1977a) used visible foliar injury including necrotic lesions, chlorosis, or pigmentation. The limiting values are based on dose-response relationships for visible injury under the assumption that if visible foliar injury is prevented, other adverse effects are unlikely. Although this assumption is not always valid, it provides the only basis for current estimates of limiting values.

With the previously discussed criteria, individual data sets were used to derive limiting values for reducing ozone-induced foliar injury to trees and shrubs (Figure 16). The presentation is based on data from: Berry (1971, 1974), Berry and Ripperton (1963), Costonis and Sinclair (1969b), Davis and Coppolino (1974a, b), Davis and Wood (1972, 1973b), Drummond (1972), Hibben (1969a, b), Hill et al. (1961), Jensen (1973), Jensen and Dochinger (1974), Jensen and Masters (1975), Ledbedder et al. (1959), Karnosky (1976), Kohut (1975), Kress (1972), Linzon (1967), Miller et al. (1969), Miller and Rich (1968), Richards et al. (1958), Santamour (1969), Wilhour (1970b), Wood and Coppolino (1972).

In Figures 16 and 17, the shaded area gives the range for the lowest ozone doses causing foliar injury to a range of plant species. Doses above and to the right of the shaded area are likely to cause foliar injury on susceptible plant species. It is unlikely that ozone doses below and to

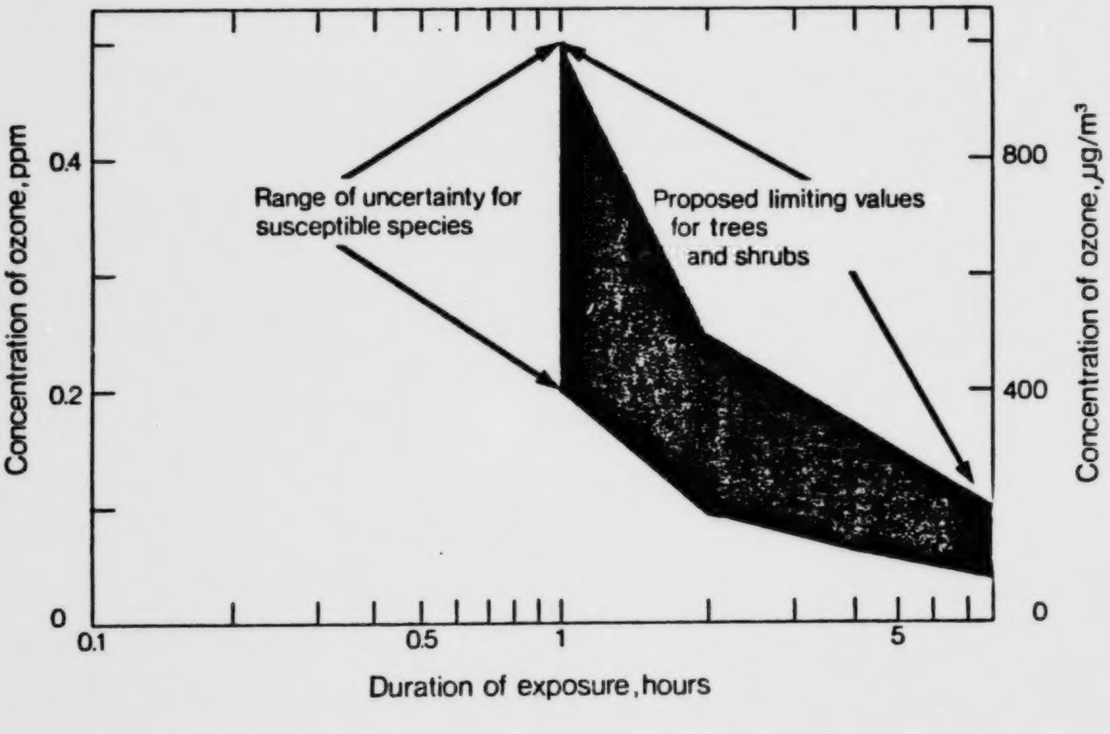

Figure 16. Proposed limiting values for foliar injury on trees and shrubs by ozone (Jacobson, 1977a).

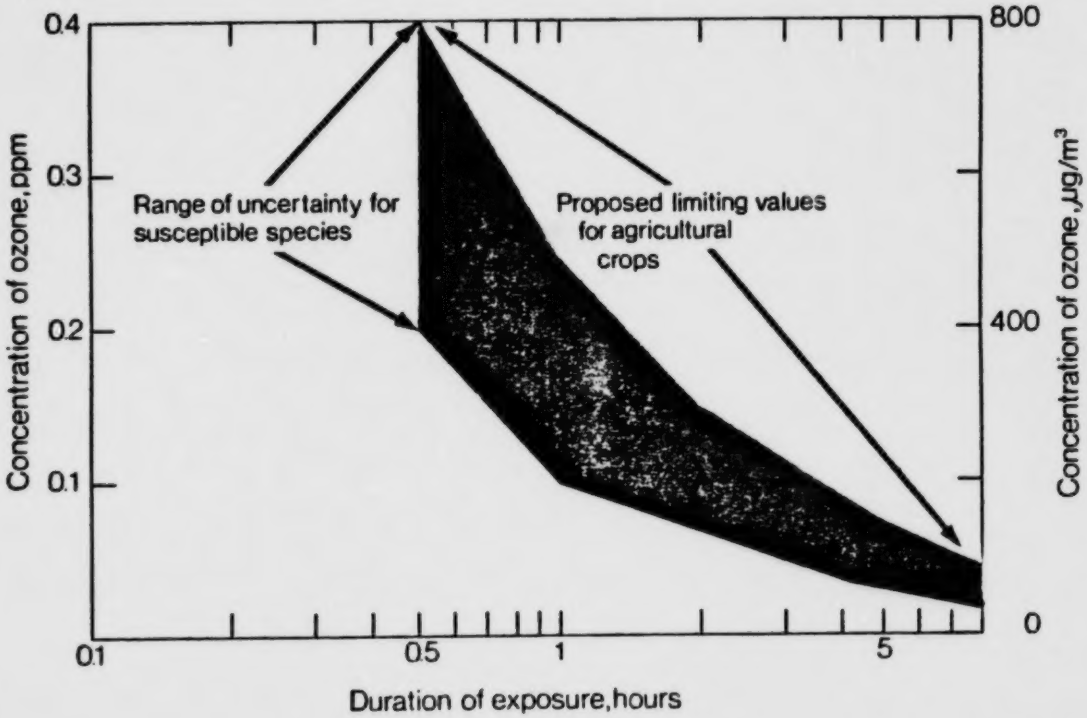

Figure 17. Proposed limiting values for foliar injury on agricultural crops by ozone (Jacobson, 1977a).

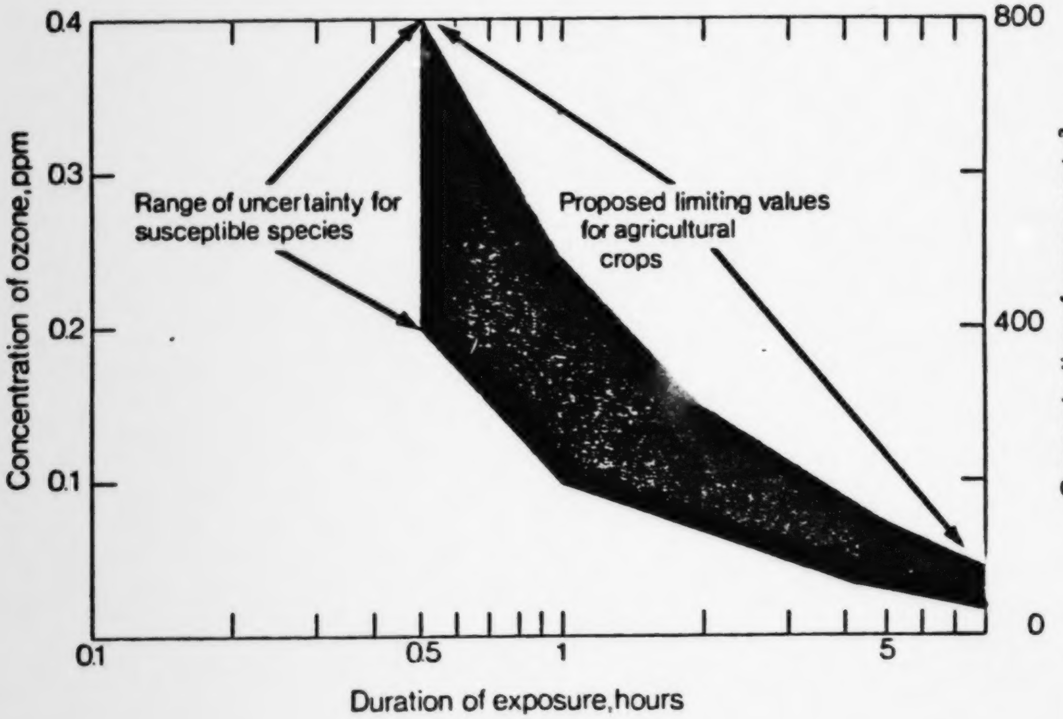

Figure 17. Proposed limiting values for foliar injury on agricultural crops by ozone (Jacobson, 1977a).

the left of the shaded area will cause foliar injury. However, certain highly susceptible clones that were selected for their ozone sensitivity may show injury at ozone doses below the curves. Data for these plants were not included because they may not be representative of the sensitivity of native and cultivated plants.

In comparison to the woody plants, there is considerably more dose-response information available for agricultural crops (compare Table 16). In Figure 17, the shaded area, representing the uncertainty range between probably harmless and injurious ozone doses, is especially large because (i) the large number of plant species tested exhibited considerable differences in their relative sensitivity and (ii) there were substantial differences in external growth conditions among the various studies. The uncertainty area includes the concentration range producing 5% injury on agricultural crops as reported by Heck and Tingey (1971) and corresponds closely to the response threshold published by Linzon _et al_. (1975).

For long term or repeated exposures, the data are not sufficient to determine if the curves in Figures 16 and 17 depart from their asymptotic approach to parallel the abscissa. Interpretations of the data for repeated or long term exposures are difficult and limiting values at concentrations less than 0.05 ppm (100 $\mu g/m^3$) are not practical because of inaccuracies in the older air monitoring equipment (Jacobson, 1977a). Until additional information is obtained, Jacobson (1977a) assumed that limiting values for exposures up to 8 h would also protect plants from foliar injury from long term or repeated exposures. Considering the mode of action of ozone, and also the possible growth reductions in the absence of visible foliar injury, such protection is not probable; however, at this time no other approaches are practical.

The range of limiting values for exposures up to 4 hours listed in Table 22 were derived from Figures 16 and 17. According to Jacobson (1977a), limiting values for exposures time > 4 h had little significance because of the difficulties in measuring low concentrations and, at longer durations, the limiting values were in the same range as the background (natural) ozone concentrations.

It is disproportionately more difficult to evaluate the potential hazards from PAN than ozone. PAN, as mentioned earlier, is the most important phytotoxic component of the family of peroxy compounds formed within the atmosphere; however, it is not the most phytotoxic. The studies of Taylor (1969) showed that peroxypropionyl nitrate (PPN) was more injurious than PAN and peroxybutyryl nitrate (PBN) was more injurious than PPN. The ambient concentrations of the PAN analogs are thought to be too small to be injurious by themselves, but they may possibly increase the phytotoxicity of PAN (Taylor, 1969).

For PAN, the dose-response data are too limited to derive separate limiting values for trees and agricultural crops (Jacobson, 1977a). Also, no range of uncertainty can be given for the doses likely to be injurious or harmless. Each coordinate in Figure 18, as with ozone, corresponds to the lowest PAN concentration and exposure duration producing foliar injury as reported in: Drummond (1972), Feder et al. (1969a), Jaffe (1967), Kohut (1975), Kress (1972), Pearson et al. (1974), Pell (1976), Starkey (1975), Wood and Drummond (1974), Wood et al. (1969). The solid line in Figure 18 provides a first approximation of limiting values for foliar injury from PAN. To the right and above the line, there is an appreciable risk of foliar injury, but for doses below and to the left there is low risk. Posthumus and Tonnijck (1982) studied the dose-response relationship of

Table 22. The range in limiting values for foliar injury from ozone on trees, shrubs, and agricultural crops (Jacobson, 1977a).

Duration h	Trees and Shrubs		Agricultural Crops	
	$\mu g\ m^{-3}$	ppm	$\mu g\ m^{-3}$	ppm
0.5			400 - 800	0.2 - 0.4
1.0	400 - 1000	0.2 - 0.5	200 - 500	0.1 - 0.25
2.0	200 - 500	0.1 - 0.25		
4.0	120 - 340	0.06 - 0.17	75 - 180	0.04 - 0.09

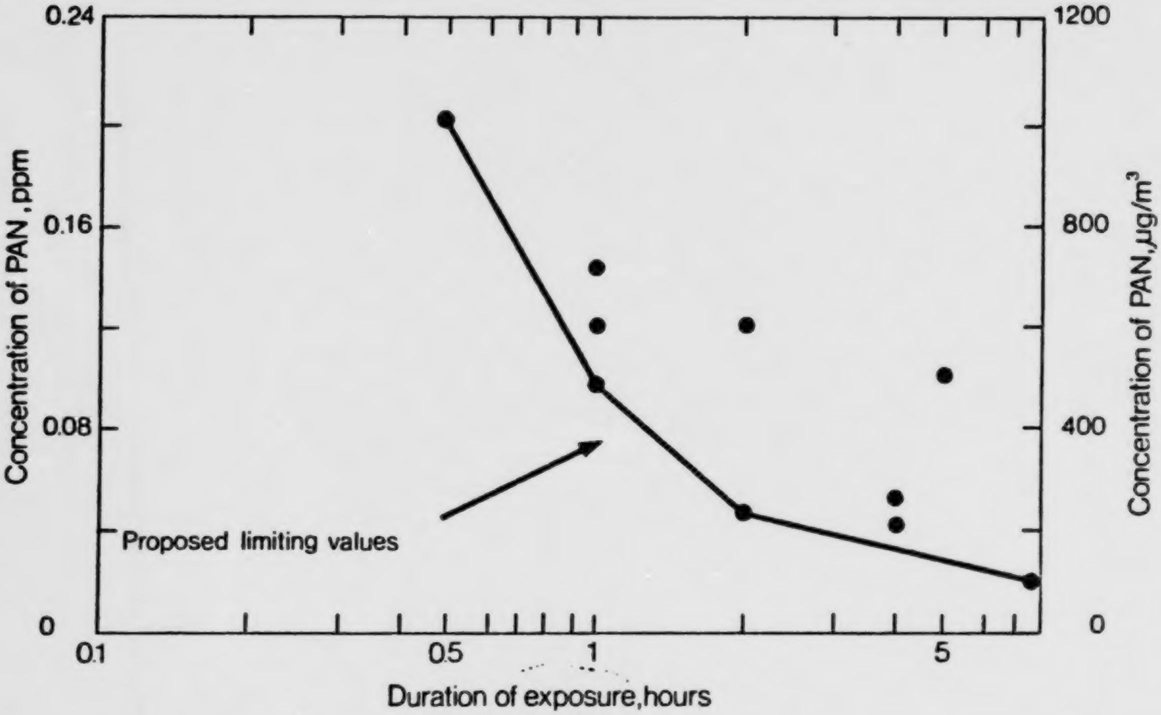

Figure 18. Dose-response relationships and proposed limiting values for PAN-induced foliar injury (Jacobson, 1977a).

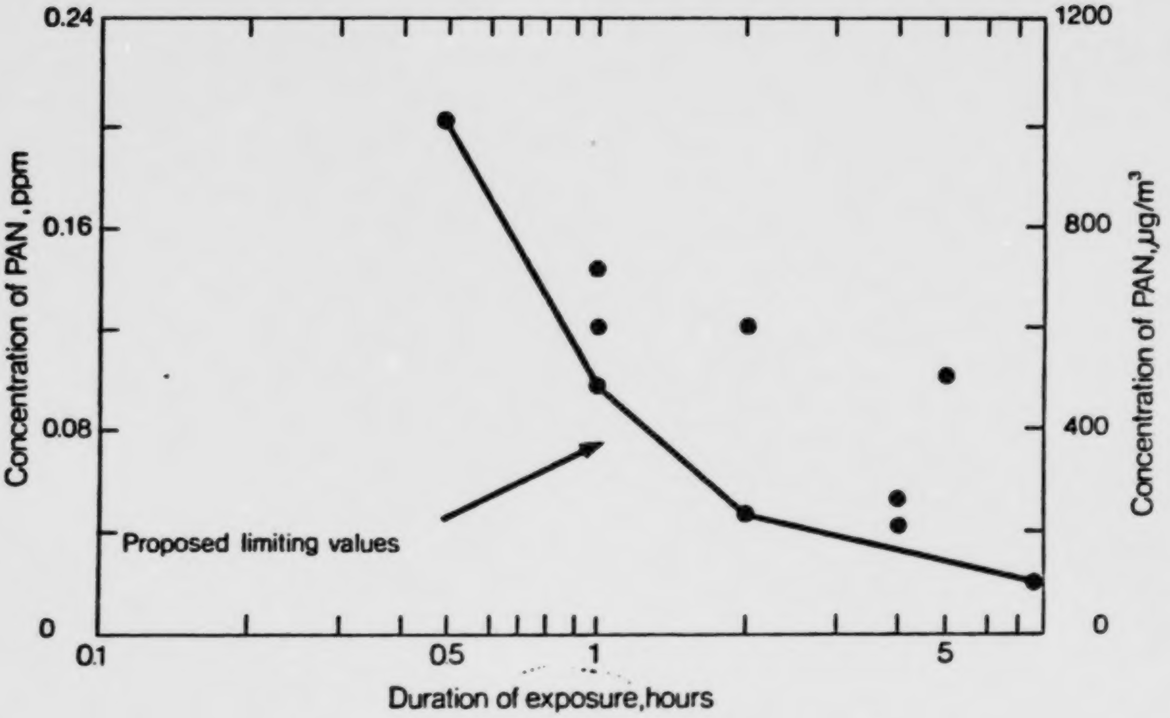

Figure 18. Dose-response relationships and proposed limiting values for PAN-induced foliar injury (Jacobson, 1977a).

little leaf nettle (Urtica urens) under conditions of maximum sensitivity. They found a similar type curve as Jacobson (1977a) (Figure 18) but the line was displaced to the left indicating that their species was more sensitive.

Jacobson (1977a) derived the following concentrations for reducing the probability of PAN-induced foliar injury:

1000 μg m^{-3} (200 ppb) for 0.5 h exposure duration
500 μg m^{-3} (100 ppb) for 1.0 h exposure duration
175 μg m^{-3} (35 ppb) for 4.0 h exposure duration

The level of protection to vegetation that would be achieved by the attainment of the air quality criteria proposed by Jacobson (1977a) cannot be determined at this time. The uncertainty results not only from limited data but also because the data were derived from controlled exposures. It is thought that plants exposed to PAN in controlled exposures are less sensitive than when exposed under field conditions. Such differences have been observed (Stephens et al., 1961; Taylor, 1969) and confirmed by others (Floor and Posthumus, 1977; Temple, 1982). In controlled PAN exposures (25 to 50 ppb, for 1 4-h exposure per week for 3 weeks), no symptoms were observed on four tomato cultivars (Temple, 1982); however, under field conditions, sensitive plants such as tomato and petunia displayed foliar injury following a 4-h exposure to 14 ppb PAN (Taylor, 1969). In contrast, Nouchi (1979), using controlled exposures, found low injury thresholds for petunia at 32, 14, and 7 ppb for 1, 3, and 8 h exposure durations, respectively.

Available data on ambient concentrations of PAN are limited, restricting the determination of possible risk to vegetation. Ambient air monitoring at Riverside, California, during 1980 for the hours of 0800 to 2000 found monthly maximum concentrations of 8.1 ppb -- July, 9.4 ppb -- September, 8.8 ppb -- October (Temple and Taylor, 1983). Hourly average concentrations greater than 30 ppb occurred 23 times between April and October. "Potentially phytotoxic eposides," defined as PAN concentrations exceeding 15 ppb for 5 hours in the morning or 25 to 30 ppb for 4 hours in the afternoon, occurred at Riverside 27 times during 1980. Along with this, PAN-induced foliar injury was observed numerous times on sensitive plant species. Based on this, concentrations for "potentially phytotoxic episodes" and limited measurements of atmospheric concentrations, it appears that PAN may endanger vegetation in only a few regions (Temple and Taylor, 1983). The ambient PAN measurements for Europe are from a few to several times less than the California concentrations (see 1._._._), and as a single atmospheric component should pose only a limited risk to vegetation (Posthumus and Tonneijek, 1982; Tonneijck, 1983a). However, it should be realized that these concentrations represent limited data from sporadic monitoring and are scarcely more than chance occurrences. Since Darley (1963) first established PAN injury on annual bluegrass (Poa annua) in the Federal Republic of Germany, repeated observations of PAN injury to many plant species in The Netherlands have been made (ten Houten, 1966; Posthumus, 1977), verifying the occurrence of phytotoxic PAN concentrations.

6.2.2 Dose Values for Definite Injury Levels

The dose-response function proposed by O'Gara (1922) has been shown to be suitable for deriving dose values that cause a defined amount of injury from short term exposures to acute injurious concentrations (compare Section 4.1). Heck and Tingey (1971) modified the O'Gara function to predict ozone injury; using this function, Linzon et al. (1975) and Heck and Brandt (1977) developed curves for definite injury levels on plants. These curves, illustrated in Figure 19, show time-concentration combinations that cause 5% injury levels. The equation for the 5% foliar injury is: c (concentration in ppm) = 0.16 + 0.12/t (t in hours) (Linzon et al., 1975). The concentration for 33% foliar injury on plants is: c = 0.21 + 0.21/t (Heck and Brandt, 1977). Larsen and Heck (1976) reviewed foliar injury data from numerous plant species and concluded: i) that a constant percentage of foliar injury was caused by a pollutant concentration that was negatively related to the exposure duration raised to an exponent and ii) for a given exposure duration, the amount of foliar injury as a function of concentration was approximated by a lognormal frequency distribution. They combined these characteristics into a mathematical model to estimate the amount of foliar injury as a function of concentration and exposure duration for a single exposure. Pratt and Krupa (1981) found a similar response in soybean.

The solid line (Figure 19) shows dose values for 5% injury on all the plants studied; the dashed line shows the threshold concentrations for sensitive plant species under conditions of high susceptibility. The individual points in the concentration-time coordinate system illustrate corresponding studies that established injury at specific ozone doses. In deriving this relationship, results from short-term controlled exposures using more than 100 plant species and cultivars were considered. The individual values used to derive the relationships (Figure 19) are shown in Table 16.

Neither the graphical representation of ozone dose based on the O'Gara function nor the limiting values (6.2.1) proposed by Jacobson (1977a) were

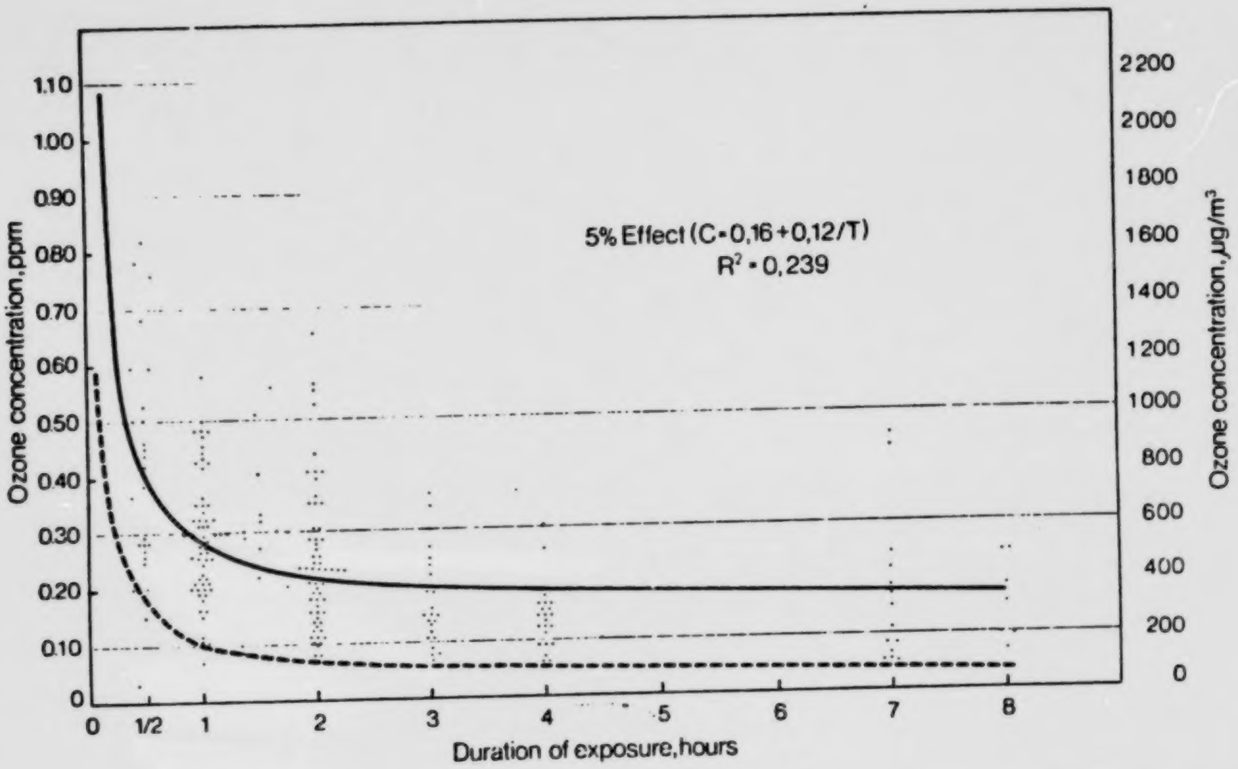

Figure 19. Concentration-time graph for foliar ozone injury developed from a single short term acute exposure to injurious concentrations using the O'Gara function: $c = a + b/t$. The solid line is the mean 5% injury level for all the species studied; the dashed line is the threshold injury level for sensitive plants (Linzon _et_ _al_., 1975).

developed to consider the differential resistance levels of individual species or cultivars. In consideration of the requirement to provide the largest possible set of decision criteria, limiting values for air quality criteria were derived for several resistance groupings (compare 4.3.2). Heck and Brandt (1977) used a modification of the O'Gara function (Heck and Tingey, 1971) to evaluate the results of ozone concentration and exposure duration on injury development from short term controlled pollutant exposure to derive the dose-response values for sensitive, intermediate, and resistant plant species (Table 23).

6.2.3 Ozone -- Maximum Acceptable Concentrations for the Protection of Vegetation

The ozone concentrations and exposure durations shown in Table 23 will induce foliar injury following a single exposure of plants grown under conditions favorable for injury development. When one considers that with repeated exposures a summation or intensification of individual effects can occur and that in the complete absence of visible symptoms growth reductions are possible, then it is obvious that even if the concentration values in Table XXIII are obtained, a considerable risk to vegetation remains. Similar conclusions were reached by Prinz and Brandt (1978) in their study for the European Community. The attainment of the concentrations and durations shown in Table 24 should guarantee a practical far-reaching protection of vegetation in its various functions, for ozone acting alone.

The numerical values in Table 24 are based on the limiting values proposed by Jacobson (1977a), and the dose-response values for definite injury levels developed by Heck and Brandt (1977) in which they used

Table 23. Ozone concentrations for short term exposures that will produce 5% detectable injury on plants of various resistance levels grown under sensitive conditions (Heck and Brandt, 1977).

Exposure Duration, h	Resistance Level: Sensitive $\mu g\ m^{-3}$	Sensitive ppm	Intermediate $\mu g\ m^{-3}$	Intermediate ppm	Less Sensitive $\mu g\ m^{-3}$	Less Sensitive ppm
0.5	400	0.20	600	0.30	1000	0.50
1.0	200	0.10	400	0.20	600	0.30
2.0	140	0.07	300	0.15	500	0.25
4.0	100	0.05	240	0.12	460	0.23
8.0	60	0.03	200	0.10	400	0.20

Table 24. Proposed maximum acceptable ozone concentrations for the protection of vegetation.

	Resistance Level					
	Sensitive		Intermediate		Less Sensitive	
Exposure Duration, h	μg m^{-3}	ppm	μg m^{-3}	ppm	μg m^{-3}	ppm
0.5	300	0.150	500	0.25	1000	0.50
1.0	150	0.075	350	0.18	500	0.25
2.0	120	0.060	250	0.13	400	0.20
4.0	100	0.050	200	0.10	350	0.18

research from North America. The question remains, if and to what extent these values can be extrapolated to Middle and Western European conditions. However, it is known that plant response is dependent on the pollutant exposure and internal and external resistance factors. In deriving the dose-response values from various experiments, it should be remembered that various edaphic and climatic conditions were used. Given this wide spectrum of conditions, it is assumed that the prevailing conditions of Middle and Western Europe are also included. From this perspective, there is no valid reason why the dose-response values developed in North America cannot be used in Europe as a basis for remedial and mitigative actions.

It is not possible to answer the question of the significance of differences in genetically controlled resistance levels between European and North American vegetation. As shown in Section 4.3.2, large resistance differences exist not only among individual species but also among cultivars and plants with different seed origins. From available data, it is not possible to determine if the resistance levels of the native and cultivated plants of Europe partially or completely overlap with the tested species from North America. However, recent studies in Holland showed that numerous European bean cultivars were as sensitive or more sensitive to ozone than a sensitive North American cultivar (Tonneijck, 1983b). Given the small difference between clearly phytotoxic ozone concentrations and the natural ozone background it appears, at least for native plants and forest stands with natural reproduction, that the assumption is justified that the resistance increases with concentrations of the natural ozone background. Plants from areas with a high ozone background would have a higher ozone tolerance. If the hypothesis is correct, then the air quality criteria determined for North American vegetation will be adequate for vegetation other countries only if it has experienced similar natural background concentrations.

An additional uncertainty in establishing dose-response values from North American findings is that dose-response relationships have been established for only the early development stages of long lived perennial plant cultures. For example, the exposure doses that will injure forest trees in the pole or mature stages cannot be determined with certainty based on the available field data (compare 4.3.1).

These important questions for deriving limiting values can only be clarified from corresponding experimental studies. Investigations of oxidant effects are necessary, especially under the relatively high SO_2 and acidic precipitation burden in Europe and other countries (see Chapter 1). For example, the decline in forest conditions in Central Europe is possibly the result of the combined effects of ozone, sulfur dioxide, and acid precipitation on forest ecosystems (see 5.5).

CHAPTER 7
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